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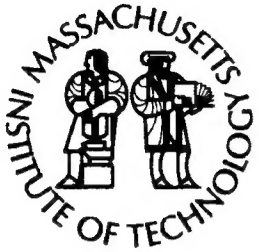

Joint Program in Oceanography/ Applied Ocean Science and Engineering

DOCTORAL DISSERTATION

Life History Traits and Population Processes in Marine Bivalve Molluscs

by

Bonnie J. Ripley

February 1998

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Cambridge, Massachusetts 02139

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Life History Traits and Population Processes in Marine Bivalve Molluscs

by

Bonnie J. Ripley

B.A. Occidental College, Los Angeles, 1992

Submitted in partial fulfillment of the
requirements for the degree of

DOCTOR OF PHILOSOPHY

at the

MASSACHUSETTS INSTITUTE OF TECHNOLOGY

and the

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Life History Traits and Population Processes in Marine Bivalve Molluscs

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Submitted in partial fulfillment of the requirements for the degree of
Doctor of Philiosophy at the Massachusetts Institute of Technology
and the Woods Hole Oceanographic Institution
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Abstract

In this thesis, I investigated the how the life history characteristics of the clam *Mya arenaria* determine the population response to chronic contaminant exposure. To predict the potential responses of a broadcast-spawning life history such as that of *M. arenaria*, I surveyed the literature on a variety of bivalve species. By incorporating information on growth, survival, and reproduction into matrix population models I could evaluate the relative contributions of these factors to fitness. For broadcast-spawners, long life is an important factor enabling them to gamble on rare, large recruitment events. Another important aspect of the broadcast spawning strategy is the possibility of high variation in larval settlement from year to year. I evaluated the role that this variability plays using a stochastic matrix model, and showed that it tends to increase population growth because of the larger size of rarer, successful recruitment events.

With an understanding of how the life history traits of *M. arenaria* might control its responses to change in the environment, I analyzed the vital rates of clams at clean and contaminated sites. The effects of contaminants measured in the lab do not necessarily predict population condition in the field. Since surviving with a long life span contributes the most to fitness in broadcast-spawning bivalves, effects on reproductive output and juvenile survival, which are strong in many lab studies, may not necessarily play a large role in field populations. The life history of this clam, with natural variation in recruitment from year to year, further reduces the population

dependence on high reproductive output and larval survival. The combination of little population-level relevance of the strongest contaminant effects, and potential contaminant effects on very important clam predators, could explain why populations at contaminated sites are observed to be growing the fastest. The interaction of contaminant exposure and normal ecological processes determines the overall impact on the population.

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Chapter 1

Introduction

1.1 Life History

Life history traits are parts of a suite of co-adapted factors that relate to survival and reproduction of an organism (Stearns, 1992). Trade-offs required between energy invested into survival and reproduction, for example, prevent organisms from having the optimal strategy of maximal reproductive success at birth. Although there is some plasticity in life history traits, the type of life history an organism has impacts how it can respond to change in the environment, such as anthropogenic contamination. For example, some species have life stages that are more sensitive to disturbances than others. Among marine bivalve species there is a broad range of life history characteristics. Some are small and short-lived, and brood few offspring, while others are longer-lived, and broadcast spawn many offspring. The latter life history is the most common in marine invertebrates in general.

1.1.1 Life History of Soft Shell Clams

The soft-shell clam, *M. arenaria*, is common and commercially important in New England. It has a life cycle typical of marine benthic invertebrates, with a sessile adult phase and a dispersive larval phase (Figure 1.1). The reproductive process

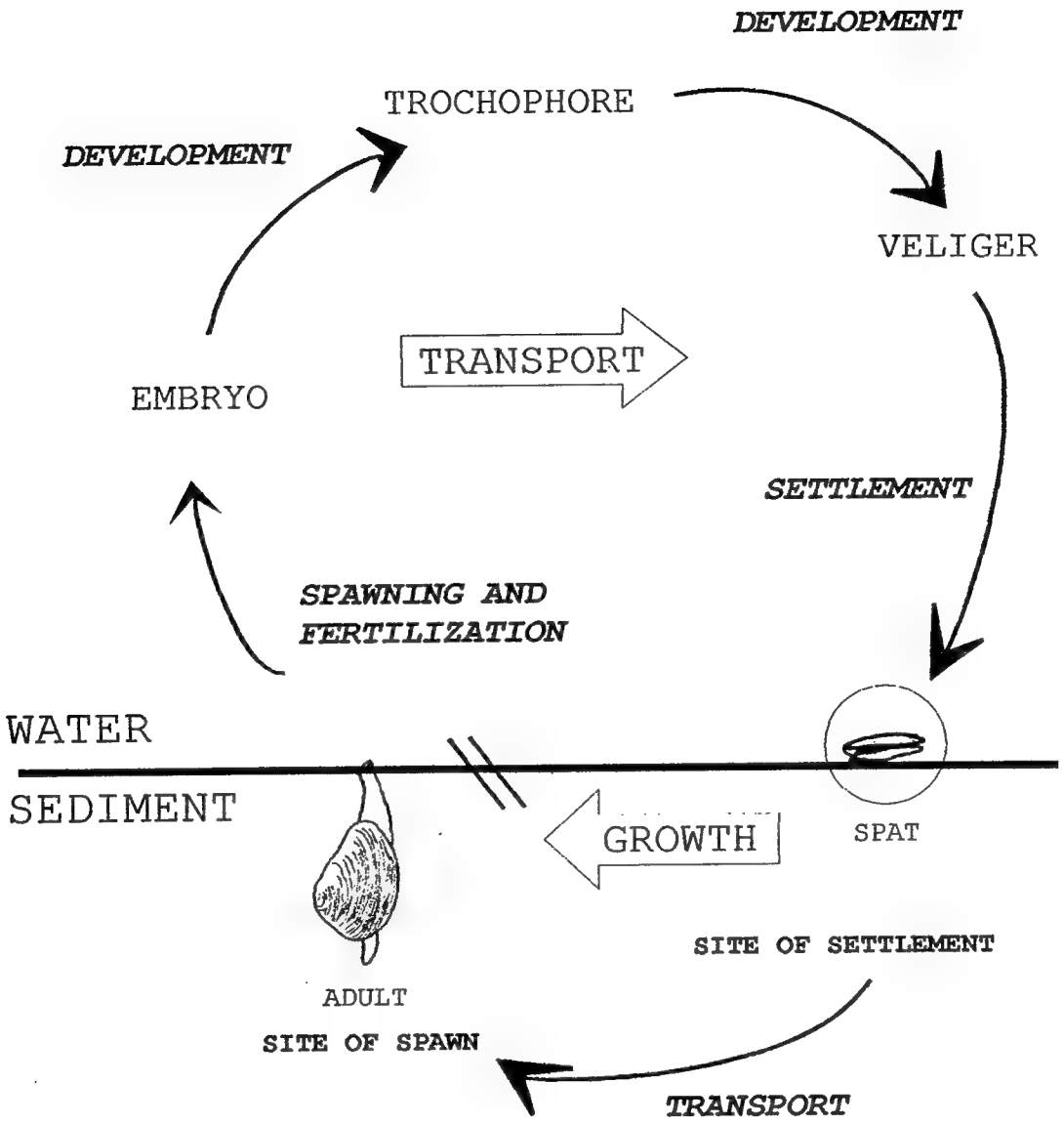

Figure 1.1: Life Cycle of *Mya arenaria*. Sessile adult and planktonic larval phases, and the processes which affect each phase, are shown.

starts in late winter, when gametogenesis begins with female clams mobilizing lipid reserves and depositing them into the developing eggs (Giese, 1959; Vassalo, 1973). The lipid pool in the egg constitutes the energy reserves that will be available to a larva during its early developmental stages. Larval survival is dependent on the maternal contributions of energy reserves: bivalve larvae from larger eggs (Kraueter *et al.*, 1982) or more lipid-rich eggs (Gallager *et al.*, 1986) have a higher chance of surviving to metamorphosis.

When water temperature rises in the spring, sperm and oocytes are shed simultaneously into the water column, where fertilization takes place. After about 12 hours, trochophore larvae form, which develop into veliger larvae about 12 hours later. Female clams produce on the order of 10^4 eggs per animal per spawning event (Brousseau, 1978), but larvae are subject to intense mortality during the planktonic period. An approximate value for larval survival is 1% (Thorson, 1966), but calculations have shown that for *M. arenaria* this value is essentially zero in some years (Brousseau *et al.*, 1982). Mortality is principally due to eggs going unfertilized, predation, starvation of larvae, and failure of larvae to find a suitable settling spot (Rumrill, 1990). Interannual variation in these factors can lead to variability in recruitment from year to year.

Planktonic larval development continues for 14–21 days after fertilization, whereupon the velum is shed and larvae settle onto the substrate. During the post-settlement period, they can continue to crawl and swim for 2–5 weeks, before settling permanently (Newell, 1991). Newly–settled clams are much more susceptible to predators and environmental stress than adults. They grow rapidly, however, and escape these mortality factors with size. Growth slows when sexual maturity is reached, at about 40 mm in size or 2 years of age, depending on water temperature and food supply (Goshima, 1982). Adult clams can live longer than 12 years (Newell, 1991).

1.2 Contaminant Effects on Bivalves

Many intertidal areas around the world are heavily contaminated with lipophilic organic compounds such as polychlorinated biphenyls (PCBs) and polycyclic aromatic hydrocarbons (PAHs). Due to their hydrophobicity, PCBs and PAHs reside in the sediment and porewater and linger in the environment even when the source is removed (Farrington, 1990). The long-term effects of such chemicals on the organisms exposed to them are currently an active area of research. Bivalves such as *Mya arenaria* are frequently used as sentinel organisms (organisms that can be easily monitored in the environment for exposure, uptake, and effects of contaminants) because they accumulate toxins readily, process them minimally, and their tissues reflect only local conditions because they are sessile (NRC, 1991).

1.2.1 Exposure and Uptake

Over the life cycle of the clam, routes of contaminant exposure and ability to absorb and store contaminants change. Adults are exposed to sediment and porewater contamination through the integument and through the gut lining from feeding on contaminated sediment. Uptake of lipophilic contaminants is controlled by simple equilibrium partitioning between concentrations in the water and those in the hemolymph and tissues, modulated by exposure duration and physiological state of the animal (Farrington, 1990). The ultimate fate of hydrophobic contaminants is storage in fatty tissues such as the gonads (Moreno *et al.*, 1992). Total tissue lipid content has been shown to dictate the amount of hydrocarbon that oysters are able to accumulate (Stegeman and Teal, 1973).

Female clams mobilize their lipid stores into egg production, so some of their stored contaminant load is shed as they spawn, causing seasonal differences in tissue contaminant concentrations (Hummel *et al.*, 1989; McDowell Capuzzo *et al.*, 1989). This transfer may only be possible for certain compounds, though; lower molecular

weight PCBs are transferred into eggs in the blue mussel, *Mytilus edulis*, but higher molecular weight ones remain in adult tissues (McDowell Capuzzo *et al.*, 1989). Most of the contaminant burden in a larva is that transferred to the egg by the mother, since only after oil spills or other pollutant input events are hydrophobic contaminants in the water column. The fate of contaminants in larval tissues as they develop and use up lipid reserves is unknown.

After settlement, juvenile clams will start to accumulate lipophilic contaminants from the environment if they are exposed to them. Experiments have shown that if bivalves are placed in flowing, clean water, they are able to depurate their tissues of low molecular weight oils in days to weeks (Widdows *et al.*, 1985; Stegeman and Teal, 1973; Moreno *et al.*, 1992). However, even low level exposures sustained over time, the most environmentally relevant scenario, cause concentrations in the animal's tissues to persist (Moreno *et al.*, 1992). Heavier oils and PCBs are more persistent in tissues. For example, PCB concentrations did not change in mussels transplanted from a contaminated site to a clean site (Hummel *et al.*, 1989).

Uptake of contaminants depends on the mixture of compounds present, and its physical and chemical bioavailablity to clams. Lower molecular weight compounds are volatile and more water soluble, and are not extensively accumulated in animal tissues, while large compounds are not assimilated because of steric hindrances in transport through membranes (Farrington *et al.*, 1986). For example, Stegeman and Teal (1973) found that petroleum hydrocarbon fractions in oyster tissues had a greater aromatic content than the oil to which they were exposed. Gardner and Pruell (1988) found that PCB congeners in *M. arenaria* tissues were of lighter molecular weight than those found in sediments. Further, concentrations in clam tissues were 2–3 times higher those found in sediments, demonstrating bioaccumulation.

1.2.2 Metabolism of Lipophilic Contaminants

Excretion of toxins and potential for damage depend on the extent of metabolic transformation of the compounds. Metabolism of lipophilic contaminants, as is known in vertebrates, is a two-step process. First, compounds undergo oxidation, reduction, or hydrolysis reactions (phase I) to expose functional groups necessary for the conjugation or synthesis reactions which constitute phase II. Initially, researchers had difficulty demonstrating ability of bivalves to transform xenobiotics but there is now evidence that they at least possess the appropriate enzyme systems. Activity of cytochrome P-450, a well-known phase I enzyme in vertebrates, has been detected in the digestive gland of mussels and clams (Stegeman, 1985; Livingstone and Farrar, 1985), although levels of activity are an order of magnitude lower than in mammals (Ribera *et al.*, 1989). Activity of other phase I enzymes has also been reported, particularly benzo[a]pyrene hydroxylase (BPH: Moore *et al.*, 1980; Anderson, 1985). These responses have all shown some level of induceability in the lab, but variability is high. In the field, no clear dose response to environmental exposure has been observed, limiting the utility of measuring phase I enzymes as biomarkers for contaminant exposure.

Most of the cellular damage from PCBs and PAHs results from the highly reactive intermediate compounds generated by the phase I reactions. Evidence of these reactive intermediate metabolites would demonstrate the extent of xenobiotic metabolism occurring in bivalves, but few researchers have studied it. Anderson (1985) found the highly mutagenic 7,8-diol BPH product in hard clams (*Mercenaria mercenaria*) exposed to Aroclor 1254, but it was also found in controls. *Mytilus edulis* converted about 17% of an aromatic amine body burden to N-acyl derivatives, which can form mutagenic DNA adducts (Knezovich *et al.*, 1988). Kurelec and Britvic (1985) showed that digestive gland microsomes of *M. galloprovincialis* also activated aromatic amines, but did not activate PAHs. The reaction was non-inducible, indicating that its normal physiological function may not relate to xenobiotics. It is

hypothesized that the lower toxicity levels often reported for bivalves may be due to their lower capacity to convert contaminants to damaging, highly reactive intermediate forms (Hale, 1989).

Reactive intermediates generated by phase I reactions are scavenged by phase II enzymes, which catalyze reactions yielding excretable hydrophilic molecules. An example of a phase II enzyme is glutathione-S-transferase (GSH), which scavenges damaging free radicals and forms hydrophilic glutathione conjugate products. A freshwater mussel showed an order of magnitude greater level of activity of GSH after exposure to dieldrin or lindane. (No metabolites of these organochlorine toxins were detected, however, suggesting that they are not actually being biotransformed: Boryslawsyj *et al.*, 1988). Ribera *et al.* (1989) found that due to higher levels of free radical scavengers (GSH, retinol, and tocopherol) and fewer activated molecules because of lower P-450 activity, *M. galloprovincialis* had the same rate of lipid peroxidation as rats. Regrettably, such measures of contaminant effects, using rates of xenobiotic metabolism, have not yet characterized bivalve responses to environmental gradients sufficiently for use in monitoring programs. Levels of heat shock proteins and DNA strand breakage are two other potential biochemical biomarkers for contaminant exposure. Results from preliminary studies of these responses suffer from incompletely-determined methodologies and poor controls, but may prove useful after further research (Clayton, 1996).

1.2.3 Physiological Effects

Correlations between contaminant exposure and various pathologies and physiological impairments have been more clearly documented. For example, the presence of a suite of histopathological disorders was sufficient to discriminate between sites grouped into three levels of contamination (Moore *et al.*, 1996). Gardner *et al.* (1991) found that laboratory and field exposure of oysters to sediment laden with PCBs, PAHs and heavy metals (including known carcinogens and tumor promoters) caused neoplas-

tic disorders after one month, while no lesions appeared in control animals. Clams in contaminated sites may be more susceptible to disease (Mix, 1988) or parasites (Gardner and Pruell, 1988) than animals in clean sites.

Effects on reproduction due to pollution exposure are linked to changes in energy storage at the cellular and organismal level. Energy budget measurements in *M. edulis* showed decreasing scope for growth with increasing PAH levels, both in the field and in mesocosm experiments (Widdows and Johnson, 1988). Oysters in areas of high PAH had lower lipid levels (Bender *et al.*, 1988), and exposure of blue mussels to hydrocarbons caused a reduction in lipid storage levels including oocyte atresia (breakdown) and resorption (Lowe and Pipe, 1987). Lowe and Pipe (1987) also showed that effects of contaminants are modulated by the energy reserves of the exposed animal. In their study, pre-spawning mussels had a mortality rate of 30% after high doses of PAH, while post-spawn mussels had a mortality rate of 70%. They hypothesized that the pre-spawn animals were able to survive better by remobilizing energy stored in gametes to meet metabolic demands, whereas this energy was no longer available to the post-spawn animals. Oocyte resorption is not a conscious choice of the organism, since it is probably due to xenobiotic-induced destabilization of lysosomal membranes. Once membranes are compromised, digestive enzymes contained in the lysosome attack the cell itself. Lipids are resorbed along with other cellular components and can then be redistributed to other tissues (Moore, 1988).

Studies determining LC_{50} values for toxicity tests have shown that environmental levels of some heavy metals (Martin *et al.*, 1981), oils (Bryne and Calder, 1977), and tri-butyl-tin-oxide (Beaumont and Budd, 1984) will kill bivalve larvae, but sublethal effects are very poorly studied. Bryne and Calder (1977) showed that high concentrations of oils caused *M. mercenaria* embryos to cease dividing and fall apart after three hours. This study also showed that if there were a decrease in survival of larvae in a treatment, there would be slower growth in the survivors. A study on larval viability in hard clams from five sites in Connecticut demonstrated increased levels of

embryo abnormalities such as chromosome stickiness at contaminated sites (Stiles *et al.*, 1991). The only other study of sublethal effects on bivalve larvae demonstrated that exposure to contaminated sediments causes failure to metamorphose in larvae of *Crassostrea gigas*, the Japanese oyster (Phelps and Warner, 1990). Despite a lack of data on the mechanisms, larvae are generally considered the most sensitive life cycle stage to contaminant exposure.

Interactions between the physiological problems discussed above remain to be determined, despite evidence that they are important. Kluytmaus *et al.* (1988) showed that the effects of cadmium exposure on *M. edulis* were both an increase in pre-spawn mortality and an increase in the number of spawning individuals. Although it is possible that these effects cancel one another out, the relative magnitudes of the changes need to be analyzed before any such generalizations are made. Further, some potential contaminant effects may seem counter-intuitive. For example, reduced egg production may actually lead to increased fertilization success, if sperm density is a limiting factor (Levitan and Peterson, 1995). This type of information reinforces the argument for studying contaminant effects in an integrated manner.

1.2.4 Effects on Population Processes

Contaminant effects may impact not only the individual, but also the population. Population growth, at the most basic level, is defined as the number of births minus the deaths. Reduction in the number of births is a proven consequence of contaminant exposure, as discussed above. The impact on the population will depend on the extent of reduction and the life history strategy of the organism. For example, the broadcast spawning bivalve life history strategy with high reproductive output and a planktonic larval phase may not be sensitive to reductions in births, since so few larvae survive to metamorphosis.

Deaths can be increased by contaminant exposure, although direct mortality from contaminant exposure is rare, except in cases of sudden high exposure, such as an oil

spill at a previously uninsulted site. Barry and Yevich (1975) and Appledoorn (1983) report cases of immediate and massive mortality of *M. arenaria* after oil spills. Dow (1975) also found that if clams were transplanted from a clean to a contaminated site, mortality was 60% higher than control rates. Timing of the exposure to chemical stress, with respect to reproductive condition and energy reserve levels, can modulate ability to survive the insult (Lowe and Pipe, 1987). Increased susceptibility to disease and environmental stresses, such as unusually cold winters, are more likely to cause increased mortality rates where chronic contamination is present.

These studies do not address the more common situation where bivalves settle and grow to maturity in a chronically contaminated environment. In this case, either genetic selection for contaminant-resistance at the metamorphosis stage, or physiological adaptation to the habitat may play a role in the health of the population. Both of these processes are possible. For example, post–settlement selection for salinity tolerance has been shown to take place in populations of *Mytilus edulis* (Hilbish and Koehn, 1985a and b). Regardless of the process generating the dominant phenotypes, differences in individual physiology between clean and contaminated sites can lead to different population characteristics.

Slower growth rates are reported commonly in hydrocarbon effects studies on *M. arenaria* (Dow, 1975; Appledoorn, 1981). The impacts of slower growth and smaller size-at-age relationships on population reproductive output over time are several. The onset of sexual maturity is more size-related than age-related in bivalves (*e.g.* Nakaoka, 1993; Newell, 1991), so age at first reproduction would increase with slower growth. Maturation time was found to be one of the more important factors in population growth rate differences between treatments in a life table response experiment on polychetes in hydrocarbon, sewage, and algal enrichments (Levin *et al.*, 1996). Whether this effect is as important in bivalves, which have much higher lifetime reproductive output and more variable larval survival, remains to be explored with modeling techniques.

Since reproductive output increases with adult size in most bivalves (*e.g.*, Peterson, 1986), slower growth rates would result in a reduced individual reproductive output. Peterson also showed, as have many others, that gonad volume increases faster than shell size, so the affect on reproductive output would be larger than expected from shell length differences. Sensitivities of population growth rate to reproduction in *M. arenaria* depend on whether the population is growing or declining. The relative importance of reproduction in the larger-sized clams increases with decreases in population growth rate (Brousseau and Baglivo, 1984). This is due to the higher reproductive contributions of larger clams.

Slower growth rates can also lead to increased predation risk, as many bivalves attain a size refuge from some predators. For example, Nakaoka (1993) showed that only small *Yoldia notabilis* (an infaunal clam) were susceptible to predation from a crab. Blundon and Kennedy (1982) demonstrated that larger *M. arenaria* obtain a refuge from blue crab predation because they can burrow deeper than smaller clams. Spending longer at smaller sizes would expose clams to predation risk for longer, reducing survival to larger, more fecund, size.

The interactions between different effects at different stages of the life cycle and their relative importance are only starting to be unravelled. A few studies have shown mixed responses to contamination, such as reduced egg numbers but increased spawning frequency, after cadmuim exposure in *Mytilus edulis* (Kluytmans *et al.*, 1988). The impact on the population would depend on the roles of survival and reproduction in the life history strategy of the organism. Investigation of population level contaminant effects has barely begun.

1.3 Matrix Population Models

Mathematical models have proven to be powerful tools in investigating complex biological processes, either as purely theoretical tools or as methods for analyzing exper-

imental data. For example, Levin *et al.* (1994) investigated population consequences of sewage enrichment on a polychaete. A demographic model of *M. arenaria* has clearly linked the disease state of individuals to effects at the population level (Weinberg *et al.*, 1997). A series of structured models on contaminant effects on populations of *Daphnia* have shown how the lipid pools of individuals mediate their response to lipophilic contaminants, and how the structure of populations made up of individuals in differing physiological states are altered by contaminant exposure (Lassiter and Hallam, 1990; Hallam *et al.*, 1990; Hallam *et al.*, 1993). In both types of studies, analysis made possible by modelling techniques has given results that extend beyond isolated experimental results.

The impact of contaminants must be evaluated at each phase of the life cycle to understand how sublethal effects on individuals can be translated to the population level. Stage-classified matrix population models integrate information on all life cycle stages particularly clearly (Lefkovich, 1965). Analysis of the model provides information on the growth rate of the population, the impact on it of certain perturbations in vital rates, and how the vital rates interrelate (Caswell, 1989). The model also allows assessment of the biological significance of statistically significant changes (Weinberg *et al.*, 1986). While other types of mathematical models can also do this, the amount of data they require is a deterrent from their application. Detailed, species-specific structured models have elucidated population processes for *Mytilus edulis* (Ross and Nesbit, 1990) and cladocerans (Nisbet *et al.*, 1989; Hallam *et al.*, 1990), but they require many physiological and environmental parameters. Matrix models are simple to analyze, and they only require data on growth, survival, and fecundity, while still providing insight into fundamental population processes. This type of model has already been used by several researchers to study bivalves (Nakaoka, 1993; Weinberg *et al.*, 1989; Weinberg *et al.*, 1996; Brousseau *et al.*, 1982; Brousseau and Baglivo, 1984, 1988; Malinowski and Whitlatch, 1988).

A special application of the matrix model, called life table response experiments

(LTREs), has been used to analyze effects of contaminants on populations of some animals (*e.g.* references in Caswell, 1989 and Caswell, 1996). LTRE analysis interprets changes in the the vital rates as the response variable to changes in environmental factors. For the polychaete *Streblospio benedicti*, hydrocarbon exposure was found to reduce fertility and increase age at first reproduction slightly, leading to a small change in population growth rate. Sewage or algal enrichment led to decreased survival, but reduced age at first reproduction by a factor of three or two, the net effect being a large increase in population growth rate (Levin *et al.*, 1994). Other LTRE studies have shown that the most obvious effect of a toxicant on the vital rates is seldom the source of that toxicant's effect on the population (Caswell, 1996).

1.4 Research Question

I investigated the population response of *M. arenaria* to chronic contaminant exposure. I approached the problem by considering the life history of this clam and how the interaction of its life history traits with environmental changes would change population characteristics. To be able to predict the potential responses of a broadcast-spawning life history, I surveyed the literature on a variety of bivalve species and incorporated information on growth, survival, and reproduction into matrix population models. This information allowed evaluation of the relative contributions of these factors to fitness (Chapter 2). The broadcast spawning strategy results in the possibility of high varation in larval settlement from year to year. I evaluated the role that this variabiliy plays using a stochastic matrix model (Chapter 3). With an understanding of how the life history traits of *M. arenaria* might control its resposes to change in the environment, I analyzed the vital rates of clams at clean and contaminated sites to test the hypothesis that population growth rates at sites with contaminants would be lower than those at uncontaminated sites (Chapter 4).

1.5 Life cycle-environment interactions determine observed contaminant effects

Results from this thesis show that the effects of contaminants measured in the lab do not necessarily predict population condition in the field. Since surviving with a long life span contributes the most to fitness in broadcast-spawning bivalves (Chapter 2), effects on reproductive output and juvenile survival, which are strong in many lab studies, will not necessarily play a large role in field populations. The life history of this clam, with natural variation in recruitment from year to year, further reduces the population dependence on high reproductive output and larval survival (Chapter 3). There was no evidence that physiological changes in clams due to contamination led to the observed population processes for *M. arenaria* at our study sites. I propose that this is due to the combination of little population-level relevence of the strongest known contaminant effects, and potential contaminant effects on very important clam predators. The interaction of contaminant exposure and normal ecological processes determines the overall impact on the population (Chapter 4).

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Chapter 2

Contributions of growth, survival, and reproduction to fitness in brooding and broadcast spawning marine bivalves

2.1 Introduction

Marine bivalves are a highly successful group of invertebrates, found from the high intertidal to the deep sea, throughout the world ocean. Their life styles in these varied environments include differences in life history traits, such as age at maturity, reproductive life span, reproductive output, and growth rates. However, a common phylogenetic history limits the extent of possible adaptations observed in bivalves. For example, the amount of energy invested in eggs is limited by the amount of space available for egg storage inside the shell. The diversity in life history strategies exhibited by this single class makes it possible to examine the demographic consequences of different sets of life history traits. Anlyzing only bivlaves controls for differences that might be due to phylogeny, which would confound a study comparing, for example,

bivalves and asteroids.

While the comparative study of life history strategies has long been recognized as worthwhile (Cole, 1954), it is data intensive and conclusive results have been difficult to obtain. Studies on groups of mammals (Promislow and Harvey, 1990), birds (Murphy, 1989), and freshwater bivalves (Way, 1988) have compared isolated life history traits, such as mortality rates or energy invested in eggs, by standard statistical methods. The majority of work incorporating multiple life history elements on more than two species at once has been done on plants (*e.g.* Grime, 1977; Silvertown *et al.*, 1993), with the exception of one study on echinoderms (Ebert, 1996).

One method of comparing life histories is to group species according to the environment in which they live, which assumes that similar environments exert similar selective forces (Southwood, 1977). This method has been applied to many species of plants, which are categorized as competitors (C), stress-tolerators (S), or ruderals (weedy species)(R) by the levels of particular traits that they display (Grime, 1977). Amounts of stress and disturbance in an environment are hypothesized to determine where each of the three types of life histories are found. A triangular plot (Figure 2.1) with C, S, and R axes emphasizes the trade-offs between these strategies. Groups of plants from similar environments tend to fall in particular regions on this plot, demonstrating that they share many life history traits.

This descriptive method and quantitative demographic methods have recently been reconciled using elasticity analysis of matrix population models (Silvertown *et al*, 1993; but see Shea *et al.*, 1994, for caveats). In a matrix population model, the life cycle of the organism is divided into stages (Figure 2.2), and transitions between these stages due to growth (G), survival (P), and reproduction (F) are estimated. These rates of transition are the projection matrix elements. The dominant eigenvalue, λ, of the projection matrix, $\mathbf{A}$, is the asymptotic population growth rate and measures average fitness of individuals in the population (Caswell, 1989). Sensitivity of λ to change in each matrix element can be calculated. Elasticities, which are the

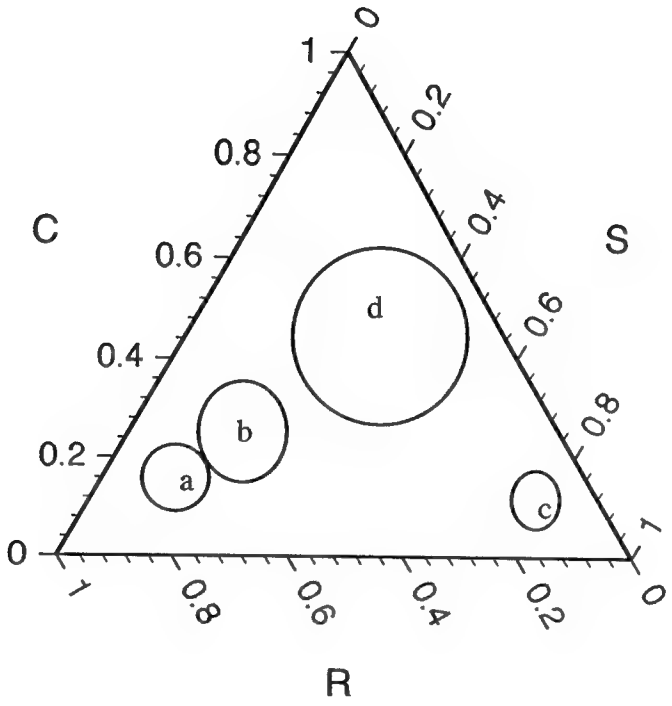

Figure 2.1: Grime's Triangle. The axes of the triangle are the levels of competetive strength (C), stress-tolerance (S), and ruderality or weediness (R) found in plant life histories. Circles show the region of CSR parameter space occupied by various groups of plants: a) annual herbs; b) biennial herbs; c) lichens; and d) trees and shrubs. Redrawn from Grime *et al.*, 1977.

proportional sensitivities of λ to changes in individual matrix elements, can also be calculated, and they always sum to one (de Kroon *et al.*, 1986). Elasticity analysis thus measures the relative contributions of different matrix elements to fitness (Caswell, 1989). By summing the elasticities of each of the three types of elements, one can identify the relative importance of growth, survival, and reproduction to fitness of individuals in a population. By equating the "competitors" of Grime's scheme to growth-maximizers, the "stress-tolerators" to survival-maximizers, and "ruderals" or fugitive species to reproduction-maximizers, the descriptive CSR scheme can be interpreted as a quantitative GPF scheme (Silvertown *et al*, 1992; Silvertown *et al*, 1993). Plotting the sums of each group of elasticities in the same type of triangular diagram (Figure 2.3) used by Grime shows the general pattern of importance of the three categories to fitness in each species.

A problem with summing elasticities to assess contributions to fitness is that although P_i are called "survival" terms, survival is included in the calculation of P_i, F_i, and G_i terms. Differences in the importance of survival for different species are confounded by simply summing types of paramerers (Enright *et al.*, 1995). This is one of the reasons that Silvertown's method of comparing elasticities is unsatisfying to some authors (Shea *et al.*, 1994). When matrix elements are calculated from terms specifying survival separately from growth, as we have done here, the elasticities to these lower-level parameters can be calculated (Caswell, 1989). This technique is used rarely in matrix modelling (*e.g.* Brault and Caswell, 1993; Levin *et al.*, 1994), and has not been applied in comparative demography because the elasticities to lower-level parameters do not necessarily sum to one (Caswell, 1989). Here, we calculate elasticities to lower-level terms m_i, σ_i, and γ_{ij} used in calculating G_i, P_i, and F_i and investigate the utility of the method in comparative demographic analysis.

The broader goal of this paper was to determine if different types of bivalve life histories have fundamentally different patterns of elasticities, and thus, different contributions to fitness by the processes represented by matrix elements. Elasticity anal-

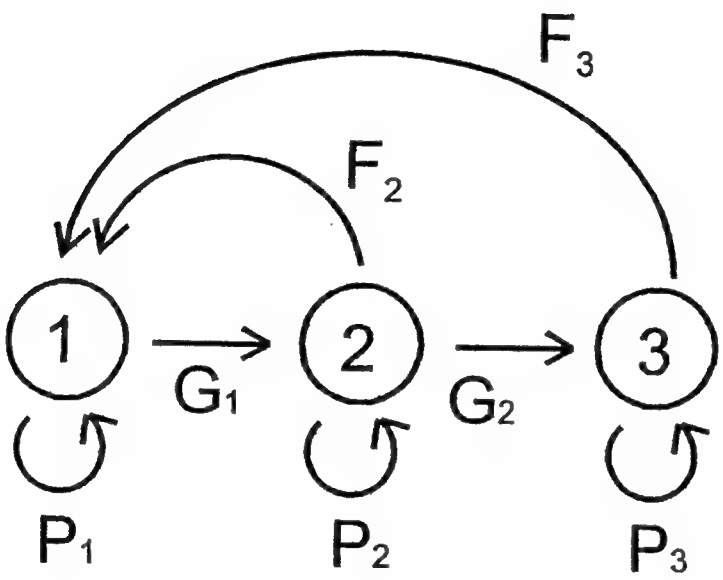

Figure 2.2: Life cycle diagram. Circles represent stages and arrows represent transitions between them over one time step. Parameters are elements of projection matrix, A.

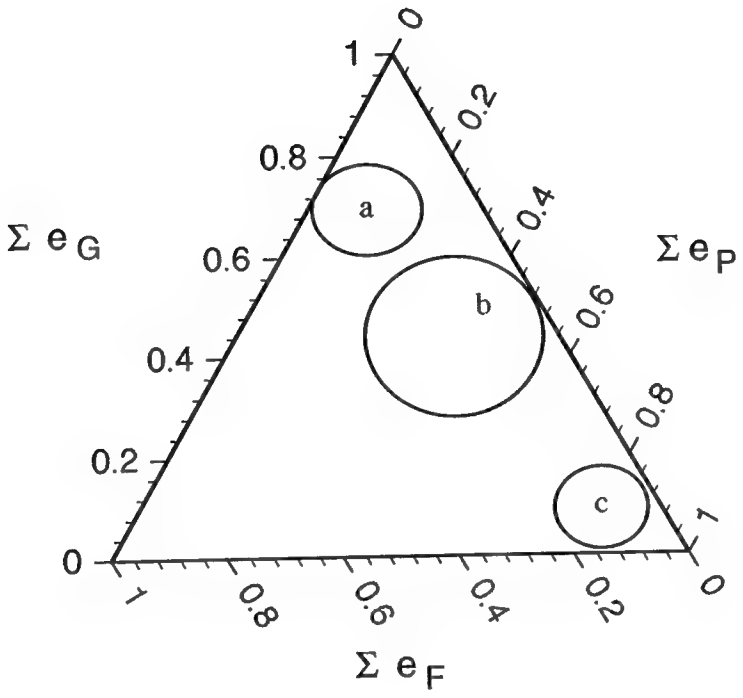

Figure 2.3: Silvertown's Triangle. Axes are the sums of elasticities to G (growth), P (stasis), and F (reproduction) parameters. The circles show regions of parameter space occupied by a) semelparous herbs; b)iteroparous herbs and c) woody plants. Redrawn from Silvertown, 1992.

ysis was performed on simple stage-classified matrix population models for ten bivalve species, over a broad range of lifestyles, parameterized with data from the literature. The discussion of our results focuses on the dichotomy between reproductive modes with broadcast spawning and those with brooded larvae. Thorson (1950) first grouped marine invertebrates into these categories. The former group releases gametes into the water column where they develop, while the latter retains the embryos within the shell for part or all of the development time, releasing benthic larvae or crawl-away juveniles. Many authors have noted that brooders and broadcasters differ most in juvenile survival (higher for brooders), fecundity (lower for brooders), and adult body size (smaller for brooders), but differences in other factors, such as life span, have not been as well studied.

2.2 Methods

2.2.1 The Model

We are interested in the relative importances of the demographic processes of growth, survival, and reproduction, to fitness in marine bivalves. We approached this problem by creating a simple demographic model in which these processes could be included, and from which fitness could be calculated. The model had to be complex enough to include the differences between the species, simple enough that it was possible to parameterize from available data, and have a form by which all the life histories could be described. In most cases, a bivalve's life span can be divided up by events such as the onset of sexual maturity, and differences in reproductive output and mortality with size. We chose to use a stage-classified model, which divided the life cycle of the bivalve into three periods of time corresponding to periods with different rates of survival and reproduction. The length of time spent in each stage depended on the life span of the organism and the timing of the life cycle events. More specifically, we defined stage one as beginning at one year from fertilization. Stage two began when

the first of the major life history events occurred, such as a substantial change in survival. Stage three began when another of these events occurred, such as attaining sexual maturity. Bivalves survived and remained in stage three with a probability that was dependent on their life span.

The equations describing the contribution of each stage to the others are:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \tag{2.1}$$

where

$$\mathbf{A} = \begin{bmatrix} P_1 & F_2 & F_3 \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{bmatrix}$$

and $\mathbf{n}$ is a vector of stage abundances. The projection interval used was one year. A set of possible transitions of this model are illustrated in a generalized life cycle diagram (Figure 2.2).

Parameters were estimated from the variety of types of data that was found, ranging from projection matrices to size-frequency histograms, which are described in detail (below) for each species. Methods applicaple to all or most species are listed in this section (Caswell, 1989). In general, reproductive contribution parameters were calculated as:

$$F_i = m_i \sigma_1 \tag{2.2}$$

where m_i is the maternity function expressed as female offspring per female and σ_1 is the probability of survival to age one. If maternity data or first-year survival probability were not available, an average recruitment of juveniles was estimated instead as:

$$F_{ave} = \frac{\text{recruits}/m^2}{\text{adults}/m^2}. \tag{2.3}$$

In this case, if the information was available, reproductive output was divided between the stages in proportion to their contribution to population reproductive output.

Growth (G_i)and stasis (P_i) parameters both include survival and both depend on stage duration. Growth parameters were calculated as:

$$G_i = \sigma_i \gamma_i \tag{2.4}$$

where γ_i is the reciprocal of the stage duration, and σ_i is an estimate of survival probability in stage i. Survival was estimated as

$$\sigma_i = e^{-\mu(x)} \tag{2.5}$$

where $\mu(x)$ is the annual mortality rate from age x to age $x+1$ (also called Z_x in fisheries literature) when these parameters were reported in the literature. The survival probablity had to be estimated in other ways in several cases, which are detailed with the parameter estimates below. Stasis parameters were estimated:

$$P_i = \sigma_i(1-\gamma_i) \qquad \text{for } i = 1, 2. \tag{2.6}$$

For $i = 3$,

$$P_3 = \exp(\frac{\ln(0.01)}{x_m - x_3}) \tag{2.7}$$

where x_m is the maximum age reported, and x_3 is age upon entering stage three. This function makes 1% of the population survive until age x_m. We identified the age which only 1% of the population attained from population age compositions or as the oldest age reported.

Parameter calculations for species for which projection matrices were available were made from these matrices. Reported annual matrices with more than three stages had to be compressed down to three stages. This was done as follows. The proportion of the population starting in each stage was calculated as the sum of the elements in the stable stage distribution falling in the stage. For each stage, the elements outside that stage in the stable stage distribution were replaced with zeros. This vector was multiplied by the annual matrix. Contributions from that stage to the others were calculated as the sum of the elements in the resulting vector falling in each stage, divided by the proportion of the population that started in that stage.

2.2.2 Bivalve Species

The species we chose to use were dictated by the availability of sufficient information to estimate model parameters. Species were chosen to represent a range of average adult size, life span, and habitat latitude and type (Table 2.1). In order to use the same model structure, which is useful in making interspecific comparisons (Enright *et al.*, 1995), all species had to have a life span of at least three years. Where ages were used, we assumed that shell growth rings are formed annually (as was assumed by the authors of literature cited here) and that populations were sampled without bias with respect to age. Finally, species were chosen if *most* of the information required to parameterize the model was avaliable in the literature. Where necessary, arbitrary estimates of missing parameters were made from anecdotal evidence.

2.2.3 Matrix Analysis

We calculated population growth rate as the dominant eigenvalue of the projection matrix. Before analyzing them further, we adjusted all projection matrices so that λ was equal to one. This was done by multiplying F_2 and F_3 by a value, k, which changed λ to equal unity. Only the reproductive parameters were adjusted since they are not only difficult to measure but may vary from year to year over wider ranges than do growth and survival (Nakaoka, 1993). The magnitude of the required changes are also biologically reasonable in the case of the reproductive parameters. This standardization is justified since the long-term average growth rate of each population must be close to one, otherwise species would tend toward extinction or overpopulation. Further, since elasiticities change depending on how fast a population is growing (Brousseau and Baglivo, 1982), setting $\lambda = 1$ eliminates differences in elasticity structure due solely to differences in population growth rate.

The remaining analyses were done on the adjusted matrices. Of principle interest

Table 2.1: Bivalve species used in this analysis, listed according to their general life history traits and environment. Question marks indicate categories for which exmaples could not be found in the literature.

	Relative Size/Life Span		
	Large/Long	Medium	Small/Short
Antarctic	none	*Adamussium colbecki*	*Lissarca miliaris* *Lissarca notorcadensis*
Temperate	*Panope abrupta* *Arctica islandica*	*Geukensia demissa* *Yoldia notabilis*	*Gemma gemma* *Lasaea rubra*
Tropical	*Tridacna gigas*	?	?
	Broadcast Spawner		Brooder

in this study were the elasticities,

$$e_{ij} = s_{ij}\frac{a_{ij}}{\lambda} \tag{2.8}$$

where

$$s_{ij} = \frac{\partial\lambda}{\partial a_{ij}} = \frac{v_i w_j}{< \mathbf{w}, \mathbf{v} >} \tag{2.9}$$

and $\mathbf{v}$ and $\mathbf{w}$ are the left and right eigenvectors of $\mathbf{A}$. Elasticities are proportional sensitivities to proportional changes in parameter values, a_{ij}. They describe how population growth rate changes with change in reproduction, growth, and survival, at the different life cycle stages of a species. Sums of elasticities to the P_i, F_i, and G_i parameters were calculated.

Derivation of the new method (H. Caswell, pers. comm.) for calculating elasticities to γ_{ij} (reciprocals of stage durations), m_i (reproductive output), and σ_i (survival probabilities) is shown in the Appendix. These types of elasticities are noted as subscripts of e; for example, elasticities to m_i are noted e_{mi}. According to the derivation, eigenvalue elasticity to the lower-level maternity parameters is simply equal to the elasticity to the higher-level fertility parameters:

$$e_{m_i} = e_{F_i}. \tag{2.10}$$

The sum of the elasticities to maternity parameters is thus equal to the sum of the fertility parameters. The elasticities to survival sub-parameters are equal to the sums of all parameters in which the survival parameter appears. Thus,

$$e_{\sigma_1} = \sum_j e_{Fj} + \sum_i e_{i1} \tag{2.11}$$

and for $i \geq 2$,

$$e_{\sigma_i} = \sum_j e_{ij}. \tag{2.12}$$

The sum of the elasticities of λ to survival will always be one, since each element of the elasticity matrix of $\mathbf{A}$ is included once in the calculation of them. Elasticities to γ_{ij} are calculated as:

$$e_{\gamma_{ij}} = e_{t_{ij}} - \frac{\gamma_{ij}}{s-1}\sum_{k\neq i}\frac{1}{\lambda}\frac{\partial\lambda}{\partial\gamma_{kj}} \tag{2.13}$$

where s is the number of stages. This type of elasticity is more complex than the others because when one γ is changed, the others in the same column must also change, since they must sum to unity. Elasticities to lower–level parameters were not calculated for *Gemma gemma* or *Yoldia notabilis* because matrices for these species were generated from matrices, not from the parameters required to calculate these elasticities.

All analyses were done using Matlab (v. 4.2, The Mathworks, Inc.).

2.3 Parameter estimation

In this section we explain how the data on each species were used to estimate model parameters. For each species, we briefly describe its natural history, list the data that was available, and note how the stages were defined. Then we detail how survival and reproductive parameters were calculated.

Adamussium colbecki–This scallop is one of the dominant species in shallow Antarctic waters (Stockton, 1984). It is anomalous as an Antarctic species in its large size (12 cm) and unprotected, planktotrophic development mode (Berkman *et al.*, 1991). Data for the model were obtained from Berkman (1990: size-frequency distributions, age v. shell height plot, data from a three-month mark-recapture survival study) and Stockton (1984: natural history). We defined stage two as beginning at two years of age because substantial mortality of small scallops had occurred between the sampling of Stockton (1984) and a previous population survey (Dayton and Oliver, 1977). We defined stage three as beginning at age five, when young scallops leave their sites of byssal attachment on the shells of larger adults and sexual maturity is reached (Berkman, 1990; S. Van Bloem, 1996). Although Berkman (pers. com.) suspects that scallops live longer than the oldest age reported, lacking any specific higher value, the maximum reported age of 20 years (Berkman, 1990) was used as the estimate of x_m. A survival rate for stage 2 scallops was estimated from the mortality

rate—three of twenty-five scallops died in a three-month period—in a mark-recapture study (Berkman, 1990). Assuming a constant survival rate over the year, annual survival was estimated as 0.56. Survival in stage one was arbitrarily estimated as 10% of that in stage 2, or 0.056. Recruitment of one-year olds was estimated by first noting that one-year old scallops are approximately 15 mm in shell height (Figure 4; Berkman, 1990). The mean over two sampling years of the ratio of scallops less than 15 mm to adults was 0.06, according to size-frequency distributions in the same paper. Assuming a 1:1 sex ratio, recruitment of female offspring was estimated as 0.03.

Arctica islandica–The ocean quahog is an infaunal, subtidal clam inhabiting muddy bottoms in shallow to deep waters of the boreal Atlantic. It can grow to 10 cm in length and to an age of 150 years (Thompson *et al.*, 1980a). Population data on the ocean quahog were obtained from Thompson *et al.* (1980 a and b: shell length, shell growth band, and gonadal condition data), and Brey *et al.*(1990: estimates of Z calculated as a regression on the length-converted catch curve). We defined stage two as starting at 7 years of age when the clams reach a size refuge from predation and have a substantially lower mortality rate than when smaller (Brey *et al.*, 1990). Stage three was defined as beginning in the tenth year of life at the onset of sexual maturity (Thompson *et al.*, 1980b). From Figure 4 in Thompson *et al.* (1980a), x_m was estimated as 142 years. The logic of dividing the population into these stages is reinforced by Brey *et al.* (1990), who found changes in the slope of the length-converted catch curve at these ages, suggesting that changes are occurring in energy allocation and mortality rates at these ages. Length-converted catch curves plot $ln(N_i/\Delta t)$ against t_i, where N_i is number of animals in the ith length class, Δt is the time spent in this length class, and t_i is age in length class i. The opposite of the slope of a regression fitted through these points is an estimate of total population mortality, Z. Mortality rates (Z_1 and Z_2) were obtained from the legend to Figure 7 in Brey *et al.*(1990) and converted to survival rates by Equation 2.5. *A. islandica* recruitment is consistently described in the literature as very poor, but not measured. An arbitrary small value,

0.001, was selected for F_3.

Gemma gemma–The gem clam is a small (ca. 4 mm) brooder which lives in temperate subtidal sand flats and has a life span of less than four years (Weinberg, 1985). We obtained data from Weinberg *et al.*(1986: population projection matrices). All three stages were defined as lasting one year, due to the short life span of this clam. All matrix parameters were calculated from projection matrices with a three-month time step reported in Weinberg *et al.* (1986). The matrix for 1978 in Table 2 of Weinberg *et al.* (1986) was selected as representative, and raised to the fourth power to obtain a projection matrix with a time step of one year. Model parameters for this analysis were calculated from the one-year matrix.

Geukensia demissa–The ribbed mussel lives in the high intertidal in the edges of peat banks, in salt marshes along the eastern coast of the U.S. It broadcast spawns annually, and can live over 15 years (Keunzler, 1961). Data were obtained from Keunzler (1961; recruits per adult, size-specific mortality rates, size at sexual maturity) and Bertness and Grosholz (1985; size at age). Sexual maturity is reached at about two years, so stage two was defined as beginning at age two (Bertness and Grosholz, 1985). Stage three was defined as beginning at age four, when there is an increase in survival rate related to reaching a size refuge from predation (Keunzler, 1961; Bertness and Grosholz, 1985). Fifteen years was estimated as x_m. Survival was estimated from Table 6 in Keunzler (1961) by first estimating that mussels in weight classes from 25–199 mg were in stage one, and from 200–799 mg were in stage two from weight–on–size regression equations (Figure 2, Keunzler,1961). Per cent mortalities for the two model stages were calculated by summing the percentages in each two-month period for three size classes in each stage, and dividing by three hundred. Two-month survival rates were calculated as one minus the mortality rates. Annual survival for the two model stages was calculated as the product of the six two-month survival rates: 0.28 for stage one and 0.71 for stage two. Recruitment was estimated as 0.44, the sum of the two-month counts of recruits per adult, divided by two to

count only females. It was partitioned equally between the two stages for lack of information on reproductive output by size.

Lasea rubra– This cosmopolitan bivalve lives in the high rocky intertidal where it occurs in Britain, on barnacle shells and in tufts of lichen. It is hermaphroditic, and broods offspring that are released as shelled juveniles each year. The largest specimens are less than 3 mm, and very few *L. rubra* live past three years of age (Seed and O'Conner, 1980). Data were obtained from Seed and O'Conner (1980; size-frequency histograms, natural history) and McGrath and O Foighil (1986; regression of brood size on shell size, reproductive condition data) Stage two begins at age two, and stage three begins at age three, since the bivalve's life is too short to partition any differently. Population densities are known to fluctuate over short time scales (Seed and O'Conner, 1980), so estimation of survival from size-frequency data would not be accurate. However, no other information was available on survival, so arbitrary estimates of $\sigma_1 = 0.5$ and $\sigma_2 = 0.8$ were made from observing the general trend in population size-structure. There tend to be high numbers of clams less than 1.3 mm, and smaller but consistent numbers of larger clams, suggesting that mortality at small sizes is higher than at large ones. In order to estimate fertilities, size ranges for each stage were estimated from size-frequency histogram in Seed and O'Conner (1980). The May panel in Figure 1 shows cohort sizes at one year from the beginning of embryogenesis. Size ranges were estimated as 0.6–1.2 mm for stage 1, 1.3–1.7 mm for stage 2, and 1.8–2.4 for stage 3. According to Table 1 of McGrath and O Foighil (1986), only a portion of the bivalves in stage 2 brood. This portion was estimated to be 0.26, as the mean (over size classes from 1.3 to 1.8 mm) proportion brooding. Number of embryos per brood, B, was estimated for the median stage sizes, $L = 1.5$ and L=2.1, from the regression:

$$B = 1.6L^{2.98} \tag{2.14}$$

(McGrath and O Foighil, 1986). According to these calculations, stage two bivalves brood 5.2 embryos, and three year olds brood about 14.6 embryos (McGrath and

O'Foighil, 1986). Multiplying the portion of stage two *L. rubra* brooding by *B* yields 1.4. Juveniles are assumed to crawl away from the parent on their first birthday so no additional mortality was imposed on the brood during this stage.

Lissarca miliaris–This sub-littoral Antarctic bivalve lives epifaunally on algae and other surfaces. It reaches a maximum size of 6 mm, with a life span of up to 7 years. *L. miliaris* broods its offspring to release as shelled juveniles annually. All of the data used below are from Richardson (1979; natural history, population size-frequencies, and size, age, and reproductive condition data). Embryos are brooded for an entire year, so juveniles enter stage one just as they are released from the parent. Stage 1 was defined as the first year post-brooding, when mortality is high. Sexual maturity is not reached until four years, so stage two was defined as the pre-reproductive period with moderate mortality–ages 2 to 4. Stage three was defined as beginning at age four and includes all sexually mature adults. Maximum age was estimated as six years, from the population size-frequency in Figure 12. Richardson (1979) assumed that the decline in numbers of individuals in the population with increasing numbers of shell growth rings was attributable to mortality. Since this bivalve is sessile, immigration and emigration are minimal and this assumption is reasonable. The mortality rate for stage 1 was estimated as 65% in the first post-brooding year, as reported by Richardson (1979, p.110). Richardson (1979) noted that less than 10% of emerging juveniles reach age four (stage 3), so survival from stage two to three was estimated at 0.53. This value brings the number of stage two bivalves to ten percent of that entering stage one after two years. Fecundity was estimated by the mean over three months of the number of recruits per adult (1.01) multiplied by 0.61, the proportion of females in the population.

Lissarca notorcadensis–This small, brooding clam lives byssally attached to the spines of sea urchins and is abundant on the Antarctic shelf and slope. Adults reach a size of about 8 mm. and live to about fourteen years (Prezant *et al.*, 1992). Data used to estimate model parameters were found in Prezant *et al.* (1992: natural

history, reproductive condition and fecundity), Brey and Hain (1992: length-at-age, size frequency distributions), and Brey *et al.* (1993: size-frequency distributions). Embryos are brooded for a year, so stage one was defined as starting at the time when juveniles crawl away from the parent, making reproductive output the number of shelled embryos brooded to release. Stage two was defined as from age two to age four. Stage three was defined as beginning at age 4 at the onset of sexual maturity. Size during the first year post-release was estimated from Brey and Hain (Figure 3) as from 1.0 mm to 2.5 mm, and during the next two years, until sexual maturity is reached, as from 2.5 mm to 4.0 mm. The age beyond which 1% of the population lives was estimated as 14 years from the size-at-age plot in Brey and Hain. Assuming that populations have a stable size structure and that there is no emigration or immigration (potentially a reasonable assumption since clams live byssally attached), decline of numbers in progressiveley larger size classes, and hence, age classes, was assumed to be due to mortality. Size frequency distributions (Brey and Hain 1992, Figure 2; Brey *et al.*, 1993, Figure 3) show that from the first year to the second year, there is a fairly sharp reduction in numbers, but after that, numbers decline much more slowly. In the population sampled, there were approximatley 14 individuals in the size categories falling in the range of first year sizes, and about 4 individuals in the size categories for the next two year classes, so survival from stage 1 to stage two was estimated as 0.29. Survival in stage 2 seems to be high, since freqencies don't show a decreasing trend during this time, so an arbitrary "high" survival rate, 0.8, was chosen for this value. Fecundity was calculated as one half of 9.4, the average brood size, assuming the population sex ratio was 1:1 (Prezant *et al.*, 1992).

Panope abrupta–The Pacific geoduck clam is infaunal and is found subtidally along the Pacific coast of North America from Baja California to Alaska. It reaches sizes up to 20 cm and can live over 100 years. Geoducks broadcast spawn annually, and population sex ratios are approximately 1:1. Data were obtained from Sloan and Robinson, (1984; natural history, histogram of age frequencies, mortality rate)

and Breen and Shields (1983; mortality rate, clam densities). Geoducks attain sexual maturity at about age five, which we defined as the beginning of stage two. By age ten, clams have essentially stopped growing in shell length, and we defined stage three as beginning at that time. Age beyond which only 1% of the population lives was estimated as 100 years from the histogram of age-frequency in Sloan and Robinson (1984; Figure 4). Mortality rates were calculated in these papers as the slope of the regression of the natural logarithm of frequency on age. Mortality rates were reported only for the whole population, not by age. Lacking mortality data by age–class, we used the highest reported mortality rate (0.035; Sloan and Robinson, 1984) to calculate σ_1 (by Equation 2.5), and the lowest reported mortality rate (0.01; Breen and Shields, 1983) to calculate σ_2. These values likely overestimate survival because only a small portion of clams sampled to generate the frequency on age curve were less than ten years old. Breen and Shields (1983) reported finding 35 clams ages 1–5 in 1,982 clams total. Assuming that those clams were evenly distributed among ages one through five, there would be seven one–year old clams present in the sample. Parameters F_2 and F_3 were both estimated as $7/1{,}982 = 0.0035$. There is likely to be a difference in reproductive output from clams in stages two and three, but as there were no data addressing this difference, no attempt was made to partition reproductive output between the stages.

Tridacna gigas–The tropical giant clam, *T. gigas* is the largest and fastest growing marine bivalve, reaching sizes up to 1 m over its 70 year life span. They live only in shallow waters, and host symbiotic zooxanthellae algae. These clams are protandric hermaphrodites, and are broadcast spawners (Beckvar, 1991). Data were obtained from Braley (1988; recrutiment rate), Munro (1988; average annual survival rates), and Pearson and Munro (1991; average annual survival rate, length-at-age data, size-frequency distributions). Stage two was defined as when clams become mature in the male phase at about 5 years, and stage three was defined as when clams become mature in the female phase at about 10 years (R. Braley, pers. com.). Maximum

age reported was 70 years (Pearson and Munro, 1988; figure 6). Survival rates were estimated for sizes of clams approximately age one and two from mean annual survival rates (Figure 8) in Pearson and Munro (1988) as 0.22 and 0.31. Survival rates through age three and four were reported in Table 1 of Munro (1988) as 0.505 and 0.635. These rates were multiplied together to obtain survival rate through stage one. Survival rates from ages 5–10 (Munro, 1988; table1) were similarly multiplied together to obtain survival through stage two. Natural recruitment in the field was measured at Michaelmas Cay, Great Barrier Reef, Australia (Braley, 1988), the same site where the survival estimates used above were measured. Recruitment observed after one year was 1.2% of the population. Only stage three, the mature females, reproduce in this model. The number of recruits was not divided by two to account for proportion females since they all become female if they survive long enough.

Yoldia notabilis–This clam is abundant in shallow soft-bottom areas in Japan. It has planktonic larvae, and reproduces annually over a relatively long lifespan (Nakaoka,1993). All data used here came from information on natural history and a Leslie matrix for *Y. notabilis* in Nakaoka (1993). Stage one was defined as ages one through three, when mortality rates are high due to predation. Stage two was defined as beginning at age four, when mortality rates are lower due to a size refuge from predation, and sexual maturity is reached. We defined stage three as beginning at age eight, which splits mature clams into two groups, the younger ones having lower reproductive outputs than the larger ones. Matrix parameters were calculated from the Leslie matrix for station YA (Table 1 in Nakaoka, 1993), using the equilibrium settlement rate for this site, 9.71×10^{-4}, as r_0.

2.4 Results

Estimated parameter values (Table 2.2) and the population growth rates calculated from them (Table 2.3) showed that while, most of the populations were not as near

equilibrium as we would expect, poulation growth rates were at least reasonable. For the broadcast-spawning bivalves, λ was equal to P_3 in some cases (ranging from 0.72 to 0.97), while for the brooding bivalves, λ varied from 0.52 to greater than one and did not correspond to any one matrix element. For most of the broadcast spawning species, values for k (Table 2.3) were large. Although population growth rates were close to one, elastisicities (Table 2.4) to F_i were small compared to those for stasis parameters, so large changes in them would be required to alter λ. The large elasticities to P_3 for broadcast-spawners also explained why this parameter determines λ for those species. In fact, P_3 always had the largest elasticity for broadcast spawners in this model, and elasticity to P_2 was always greater than to P_1.

For any given species, elasticities to early and late growth (G_1 and G_2) were nearly equal, regardless of any difference in magnitude of G_1 and G_2. For brooders, elasticities to growth and late reproduction (F_3) were the highest, except for *L. notorcadensis*. *L. notorcadensis* lives the longest of the brooders analyzed—eight years longer than the next most long-lived. Its P_3 parameter was larger than for other brooders, and the largest in the matrix. The short–lived broadcaster, *G. demissa* showed a similar pattern, suggesting that life span, not reproductive mode, was determining elasticity structure in these models.

When elasticities were summed by type of parameter, the largest sum for all species with life spans of about 14 years or more (including the long-lived brooder) was of stasis parameters, P, while for the shorter lived species it was growth parameters, G. The general pattern of elasticity structure (Figure 2.4) showed the smallest brooders clearly separated from the largest broadcast-spawners, but there was a region in the center of the plot in which they both occurred.

Calculation of elasticities to lower–level parameters(Table 2.4) had mixed results. The elasticities to m_i were the same as to the F_i, so this method offered no improvement over the standard method for those parameters. Since the elasticities to σ_i always sum to one, comparing their sum between species is useless. However,

Table 2.2: Parameter Estimates. Estimated parameter values for calculation of matrix elements: x_2 and x_3 are ages at the beginning of stages two and three, and x_m is the maximum age, γ_i are reciprocals of stage durations, and σ_i are survival rates; and calculated matrix elements: P_i, G_i, and F_i. Dashes indicate parameters which were not estimated for a species. The model for *G. gemma* includes two additional parameters: $G_{1,3} = 0.03$, and $F_{2,3} = 0.452$.

Species	x_2	x_3	x_m	γ_1	γ_2	σ_1	σ_2
A. colbecki	2	6	20	1.0	0.25	0.056	0.56
A. islandica	7	10	142	0.143	0.333	0.633	0.942
G. gemma	2	3	4	–	–	–	–
G. demissa	2	4	15	1.0	0.5	0.28	0.71
L. rubra	2	3	4	1.0	1.0	0.5	0.8
L. miliaris	2	4	6	1.0	0.5	0.35	0.53
L. notorcadensis	2	4	14	1.0	0.5	0.29	0.8
P. abrupta	5	10	100	0.2	0.2	0.97	0.99
T. gigas	5	10	70	0.2	0.0167	0.0219	0.0465
Y. notabilis	4	8	15	–	–	–	–

Species	P_1	P_2	P_3	G_1	G_2	F_2	F_3
A. colbecki	0	0.375	0.72	0.056	0.185	0	0.03
A. islandica	0.542	0.628	0.966	0.091	0.314	0	.001
G. gemma	0.296	0.134	0	0.09	00035	1.62	0.452
G. demissa	0	0.355	0.66	0.28	0.355	0.22	0.22
L. rubra	0	0	0.01	0.5	0.8	1.4	14.6
L. miliaris	0	0.265	0.1	0.35	0.265	0	0.62
L. notorcadensis	0	0.4	0.63	0.29	0.4	0	4.7
P. abrupta	0.776	0.792	0.95	0.194	0.198	0.0035	0.0035
T. gigas	0.0175	0.456	0.926	0.00438	0.00777	0	0.012
Y. notabilis	0.07	0.68	0.0797	0.003	0.17	33.12	7.25

Table 2.3: Annual population growth rates, λ, of bivalve populations (before adjusting parameters), and constant, k, used to adjust fertility parameters prior to calculating elasticities.

Species	λ	k
A. colbecki	0.72	563
A. islandica	0.97	204
G. demissa	0.75	2.88
G. gemma	0.66	3.38
L. rubra	1.93	0.15
L.miliaris	0.52	11.5
L. notorcadensis	1.19	0.4
P. abrupta	0.95	13.8
T. gigas	0.92	9.5×10^4
Y. notabilis	0.82	2.88

Table 2.4: Eigenvalue elasticities of adjusted matrices. Matrix elements are found in Table 2, but F_i have been multiplied by k (Table 3) prior to calculating elasticities. For placement of each element in the displayed arrays, see definition of **A** with Equation 2.1.

A. colbecki	0	0	0.1620
	0.1620	0.0972	0
	0	0.1620	0.4167
A. islandica	0.0345	0	0.0292
	0.0292	0.0486	0
	0	0.0292	0.8293
G. demissa	0	0.1207	0.1260
	0.2467	0.1358	0
	0	0.126	0.2447
G. gemma	0.1562	0.3469	0.0246
	0.3018	0.0538	0.0461
	0.0679	0.001	0
L. rubra	0	0.0365	0.3079
	0.3445	0	0
	0	0.3079	0.0031
L. miliaris	0	0	0.2880
	0.2880	0.1039	0
	0	0.2880	0.0320
L. notorcadensis	0	0	0.1862
	0.1862	0.1242	0
	0	0.1862	0.3171
P. abrupta	0.1373	0.0080	0.0316
	0.0396	0.1509	0
	0	0.0316	0.6010
T. gigas	0.0011	0	0.0610
	0.0610	0.0530	0
	0	0.0610	0.7630
Y. notabilis	0.0177	0.2265	0.0092
	0.357	0.5009	0
	0	0.0092	0.0008

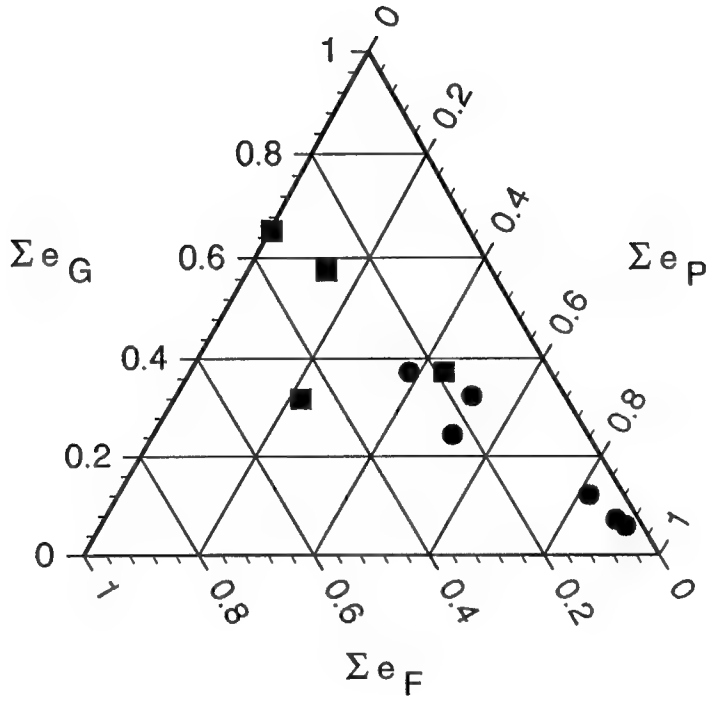

Figure 2.4: Elasticity Structures of Bivalve Life Histories. The sums of elasticities to P_i, F_i, and G_i plotted against one another. The squares are brooding species; the circles are broadcasting species. Note that only two of the variables are independent as all elasticities sum to one.

Table 2.5: Elasticities to lower–level parameters. For each species, elasticities to stage transition probability, γ_{ij}, and survival probability, σ_i are shown. Elasticities to m_i are not shown because they are the same as elasticites to F_i (Table 2.4).

Species	$\sum \gamma ij$	σ_1	σ_2	σ_3
A. colbecki	0.4792	0.3241	0.2593	0.4167
A. islandica	0.3716	0.0929	0.0778	0.8293
G. demissa	0.3415	0.4935	0.2618	0.2447
L. rubra	0.2378	0.689	0.3079	0.00511
L. miliaris	0.0604	0.5761	0.3919	0.032
L. notorcadensis	0.3862	0.3725	0.3104	0.3171
P. abrupta	0.3405	0.2165	0.1825	0.0601
T. gigas	-9.9104	0.123	0.114	0.763

comparing the pattern of σ_i values from one species to another had similar results to the standard elasticity analysis: elasticity to σ_1 was highest for brooders, while for most broadcasters, elasticity to σ_3 was highest. As we calculated them, it was possible for elasticities to γ_i to be negative, indicating that elasticity to other parameters in the same column is higher. They also measured elasticity to stage durations, which in these models were set rather artificially. So in this example, elasticites to γ parameters were difficult to interpret.

2.5 Discussion

There is a continuum of contributions to λ by stasis parameters for the species analyzed here, but as strategy changes from brooding and broadcast spawning the pattern

shifts from fitness depending on growth and fecundity to it depending on stasis. Our results suggest that the longer the life span, the less important reproduction and early growth are in the life history, regardless of reproductive mode. Menge (1977) made a back-of-the-envelope calculation to show that the small, brooding, asteroid, *Leptasterias hexactis* would have to have a life span of over 1500 years to be successful as a broadcast spawning species. This is due to the small volume available for egg production and low survival of planktonic larvae. While it makes sense for small size to constrain bivalves to brooding, it is less clear why larger sized animals do not brood. Life history analyses on ophiuroids have also shown that even for a brooding species, selection pressure appears to be towards long adult life span (Medeiros-Bergen and Ebert, in prep). After comparing various asteroid life histories, Ebert (1996) suggested that an important factor in reproductive mode is the negative relationship between larval survival and life span.

Although parameter estimates made for this analysis were from data that were, in most cases, not collected for demographic modeling, it was still possible to calculate approximate matrix parameters. A lack of appropriate data is blamed for the limited analyses that have been done to compare life history strategies, but we have found that although the data were not ideal, there are more available than has been previously utilized. We found that while fecundity data were commonly reported, growth and survival were not generally measured for different size classes, and that the biggest gap in the literature was in information on juvenile survival and recruitment. The results presented here offer an improvement over the purely statistical comparisons of life history traits as done, for example, by Way (1988), in that they combine the different elements of a life history strategy and examine them as an integrated unit, rather than as separate parts.

Growth rates of bivalves are known to vary depending on their microhabitat (*e.g.* Bertness and Grosholz, 1985). Survival (*e.g.* Weinberg, 1985) and recruitment (*e.g.* Braley, 1988) are also known to vary spatially and temporally. The projection ma-

trices calculated here are mere snapshots of a range of possible population processes for these species. Our object in calculating them was only to capture the salient life history features in general. Studies that have examined the effects of variation in matrix elements have shown that including variation can lead to changes in population growth rates (reviewed in Nakaoka, 1996). However, if we assume that variation acts similarly on the different species compared here, it can be ignored and the life histories can be compared as outlines representative of types of species.

Enright *et al.* (1995) demonstrated that either holding the number of stages constant between species or holding the time spent in stages constant between species allows meaningful comparisons to be made between species. Limited data forced us to hold the number of stages constant, and this approach tends to increase the apparent relative importance of stasis in the life history because more individuals remain in each stage every time step, and less proceed to the next stage (Enright *et al.*, 1995). Our analysis does pinpoint life span as a potentially important life history trait. However, the alteration in elasticities due to collapsing life cycles to fewer stages is not large enough(see Figure 3 in Enright *et al.*, 1995) to alter the general patterns, and it tends to shift all species in the same direction.

Elasticity patterns fall along a line over only a portion of the range in the sum of elasticity to F_i. One might have expected that brooding species would have higher elasticities to reproduction, since juvenile survival is higher, but this was not the case. Reproductive output did not contribute the most to fitness in either type of life history. It is possible that bivalves are architecturally constrained in their life history strategies to this region of the plot. However, we only used ten species in this analysis–a minute sample size. The exclusion of species with life spans shorter than three years definitely biased the outcome away from the bottom left corner of Figure 2.4, where reproduction is the most important factor. More data, especially on tropical species, which can grow very fast but have short life spans, would be likely to fill in the gaps of diversity of bivalve life histories.

Analyses on plants (Silvertown *et al.*, 1993) have shown that they cover more regions of the elasticity space than do bivalves, however, the plants analyzed represent many classes and the species analyzed here are all in Bivalvia. The plants clearly show distinct ecological groupings in demographic G–P–F space, in a similar manner to the patterns demonstrated by Grime (1977) in trait C–S–R space. Brooding bivalves fall into the same region in elasticity space as do semelparous and iteroparous herbs, while the larger broadcasters fall into the same region as do woody plants (Silvertown *et al.*, 1993). Silvertown suggests that the G–P–F method is valuable because fitness consequences of the life history can be directly interpreted from it.

The method described here to calculate elasticites to lower–level parameters had mixed results. We think that elasticities to σ_i are potentially useful in comparative demography, while elasticities to m_i and γ_{ij} were not informative. Because of dissatisfaction with the fact that elasticites to P and G parameters confound survival and growth, it is worth pursuing alternative methods of calculating elasticities to lower–level parameters further.

One of the main points of Grime's triangle scheme is that the three types of life history strategies are found in species occupying particular habitats. The link between the environment and the strategy of the plant is assumed to be tight. For bivalves, this connection is not obvious. Thorson (1950) suggested that environmental factors at different latitudes and water depths determine the reproductive strategy of marine invertebrates, but many counterexamples have been discovered more recently. The proportion of bivalve species that brood may be higher in communities in the Antartic and the deep sea (Grahme and Branch, 1985), but other life histories are present as well. Brooding and broadcasting species are found in all environments, whether categorized by latitude or by tidal level. The tropical giant clam has essentially the same contributions to fitness from different parts of its life history strategy as the temperate geoduck clam or the Antarctic scallop. Brooders are found in the high intertidal, a very stressful environment, but so are broadcasters. We do not

think that the aspect of comparative life history strategy dealing with correlations to environmental types is as applicable to marine species as to plants.

Key differences in brooding and broadcast spawning life histories may relate to time scales of variability. The longer the life span, the less important reproductive success is in each year. Long life spans may have led to the possibility of lower investment into riskier reproductive patterns. On the other hand, reduced energy investment in reproduction may allow long life. Other authors have contemplated this marked difference in reproductive mode by asking the questions: "what are the costs and benefits of having planktonic larvae?" (Grahme and Branch, 1985), "brood or broadcast?" (Menge, 1975), or "to brood or not to brood?" (Strathmann *et al.*, 1984). Perhaps the question to ask is: "How long to live?" The answer to this quesion may depend on the regime of variability in the environment (Strathmann and Strathmann, 1982). Amount of selection pressure on life span may also contribute to evolutionary outcomes. Further work incorporating variability into demographic models on life history strategies may be able to address this question.

2.6 Summary

1. We suggest that there are more data available for comparative demography than have been utilized, and that although the data may not have been collected for parameterizing models, they are adequate for theoretical analyses.

2. Survival is important to both brooders and broadcasters, but long life span contributes the most to fitness in broadcast spawning bivalves, and growth is more important to the brooders. There is a region of elasicity space where both brooders and broadcasters are found.

3. Patterns of elasticity distributions in marine bivalves apparently do not correlate to environmental conditions as do those of plants.

4. A new method for calculating separate elasticities to growth and survival was derived and used on these models.

2.7 References

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2.8 Appendix

Derivations of elasticities to the lower–level parameters m_i, γ_{ij}, and σ_i (from which projection matrix parameters P_i, G_i, and F_i are calculated) are shown below (H. Caswell, pers. comm.). These elasticities were derived in order to try to calculate elasticities to survival seperately from growth and reproduction, which is not possible by calculating elasticities to projection matrix parameters.

Let

$$\mathbf{A} = \mathbf{T} + \mathbf{F}$$

where

$$\mathbf{T} = \begin{bmatrix} \sigma_1\gamma_{11} & \dots & \sigma_k\gamma_{1k} \\ \vdots & & \\ & & \vdots \\ \sigma_1\gamma_{k1} & \dots & \sigma_k\gamma_{kk} \end{bmatrix} \tag{2.15}$$

and

$$\mathbf{F} = \begin{bmatrix} \sigma_1 m_1 & \dots & \sigma_k m_k \\ 0 & & 0 \\ \vdots & & \\ & & \vdots \\ 0 & \dots & 0 \end{bmatrix}. \tag{2.16}$$

For σ_i where $i = 1$, sensitivities are

$$\frac{\partial\lambda}{\partial\sigma_1} = \sum_{j=1}^{k} \frac{\partial\lambda}{\partial F_j}\frac{\partial F_j}{\partial\sigma_1} + \sum_{j=1}^{k} \frac{\partial\lambda}{\partial t_{j1}}\frac{\partial t_{j1}}{\partial\sigma_1} \tag{2.17}$$

$$= \sum_j \frac{\partial\lambda}{\partial F_j} m_j + \sum_j \frac{\partial\lambda}{\partial t_{j1}}\gamma_{j1}. \tag{2.18}$$

For $i \geq 2$,

$$\frac{\partial\lambda}{\partial\sigma_i} = \sum_j \frac{\partial\lambda}{\partial t_{ji}}\frac{\partial t_{ji}}{\partial\sigma_i} = \sum_j \frac{\partial\lambda}{\partial t_{ji}}\gamma_{ji}. \tag{2.19}$$

Sensitivities for m_i are simply

$$\frac{\partial\lambda}{\partial m_i} = \sigma_i \frac{\partial\lambda}{\partial F_i}. \tag{2.20}$$

Sensitivities to γ_{ij} are:

$$\frac{\partial\lambda}{\partial\gamma_{ij}} = \frac{\partial\lambda}{\partial t_{ij}}\frac{\partial t_{ij}}{\partial\gamma_{ij}} = \frac{\partial\lambda}{\partial t_{ij}}\sigma_j. \tag{2.21}$$

Elasticities to different parameters are noted as subscripts to the letter e, for example e_{m_i} are elasticities to m_i.

$$e_{m_i} = \frac{m_i}{\lambda}\frac{\partial\lambda}{\partial m_i} = \frac{m_i\sigma_i}{\lambda}\frac{\partial\lambda}{\partial F_i} = \frac{F_i}{\lambda}\frac{\partial\lambda}{\partial F_i} = e_{F_i}. \tag{2.22}$$

For $i = 1$, elasticities to σ_i are

$$e_{\sigma 1} = \frac{\sigma_1}{\lambda}\frac{\partial \lambda}{\partial \sigma_1} = \sum_j \frac{\partial \lambda}{\partial F_j}\frac{\sigma_i m_j}{\lambda} + \sum_j \frac{\partial \lambda}{\partial t_{j1}}\frac{\gamma_{j1}\sigma_1}{\lambda} = \sum_j e_{F_j} + \sum_j e_{t_{j1}}. \tag{2.23}$$

For $i \geq 2$, elasticities to σi are

$$e_{\sigma_i} = \frac{\sigma_i}{\lambda}\frac{\partial \lambda}{\partial \sigma_i} = \sum_j e_{t_{ji}}. \tag{2.24}$$

For γ_{ij}, elasticities calculated in the same manner as those above are:

$$e_{\gamma_{ij}} = \frac{\gamma_{ij}}{\lambda}\frac{\partial \lambda}{\partial \gamma_{ij}} = \frac{\partial \lambda}{\partial t_{ij}}\frac{\gamma_{ij}\sigma_j}{\lambda} = e_{t_{ij}}. \tag{2.25}$$

However, when one γ is changed, the others in the same column must also change, since they sum to one, so Equation 2.25 is not entirely correct. Suppose

$$\Delta\gamma_{kj} = \frac{-\Delta_{ij}}{s-1} \tag{2.26}$$

where s is the number of stages. Then

$$e_{\gamma_{ij}} = e_{t_{ij}} - \frac{\gamma_{ij}}{s-1}\sum_{k \neq i}\frac{1}{\lambda}\frac{\partial \lambda}{\partial t_{ij}}. \tag{2.27}$$

Chapter 3

The role of recruitment variability in determining population growth rate of the soft-shell clam

3.1 Introduction

The life history of the clam *Mya arenaria*, like that of many benthic marine invertebrates, includes a sessile adult stage that broadcasts large numbers of gametes into the water column. A female *M. arenaria* may shed up to 10^6 eggs in the spring and the fall (Brousseau, 1978), but high mortality rates and transport away from the site can result in undetected settlement of spat, despite such high reproductive output (Brousseau *et al.*, 1982). Stochasticity in environmental factors, such as wind forcing of currents, that affect planktonic larvae can cause dramatic spatial and temporal variability in settlement (*e.g.* Goshima, 1982; Vahl, 1982; Bachelet, 1986). Mortality rates of planktonic larvae also vary interannually due to their dependence on multiple biological and physical factors (Rumrill, 1990).

Variabilty in recruitment is an important phenomenon in and of itself, rather than just an irritant to field biologists (Fogarty, 1993a). We loosly define "recruits" as re-

cently settled or obviously young–of–the–year individuals. Uncertain juvenile survival is generally found in organisms with iteroparity and high fecundity (Murphy, 1968). *M. arenaria* lives for up to twelve years (Newell, 1991), so successful recruitment is not necessary each year to maintain populations (Goodman, 1984). This combination of life history traits results in what is termed the "storage effect," where population growth rate is more strongly affected by conditions favorable to recruitment success than by unfavorable ones. This effect has been shown to be important in the context of interspecific competition (*e.g.*, Warner and Chesson, 1985). In this paper, we examine the effects of recruitment variability on population dynamics of *M. arenaria*, using a stochastic matrix population model.

Matrix population models have been applied to *M. arenaria* to calculate sensitivity to changes in vital rates (Brousseau and Baglivo, 1984), and to assess disease impact (Weinberg *et al.*, 1996) and fisheries management strategies (Malinowski and Whitlatch, 1988). These studies have all used deterministic models that neglect the effects of variability. Brousseau and Baglivo (1984) and Malinowski and Whitlatch (1988) used an assumption of constant population size to estimate the "equilibrium settlement rate." This value is defined as the proportion of eggs spawned that must successfully develop and survive to their first year to produce a constant population size when combined with all the other vital rates. Settlement in this sense is what we examined to study variation in recrutiment. Since the population is assumed to be at equilibrium in these models, only equilibrium settlement rate can be compared among sites, conditions, or studies, not population growth rates. Brousseau *et al.*(1982) calculated that, for a Cape Anne, Massachusetts population of *M. arenaria*, only 0.0001% of eggs, or about one recruit or settler for every ten adults, needed to survive each year to maintain constant population size. No set at all was detected in two out of the three years, however, so in order to maintain the population, a much higher settlement must occur occasionally.

To compare previous work to the stochastic model presented here, we first formu-

lated a deterministic model. A deterministic matrix population model can be written as

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \tag{3.1}$$

where $\mathbf{n}$ is a vector of stage abundances and $\mathbf{A}$ is a constant projection matrix. The projection matrix elements are estimates of the possible transitions between stages, over one time step. The time step chosen is often one year. An annual projection matrix can also be constructed from matrices describing seasonal transitions. For example, a population can be projected from one spring to the next by a matrix:

$$\mathbf{A} = \mathbf{A}_{spring}\mathbf{A}_{winter}\mathbf{A}_{fall}\mathbf{A}_{summer} \tag{3.2}$$

where the seasonal matrices describe vital rates over portions of the year. For example, $\mathbf{A}_{spring}$ describes growth and survival from March to June. The other matrices are similarly defined over three month intervals. This approach makes it possible to include data on a finer than annual time scale into a model with an annual time step.

The dynamics of the population are determined by the matrix $\mathbf{A}$ (Caswell, 1989). The dominant eigenvalue of $\mathbf{A}$, λ, gives the population growth rate. The corresponding right eigenvector $\mathbf{w}$ and left eigenvector $\mathbf{v}$, defined by

$$\mathbf{A}\mathbf{w} = \lambda\mathbf{w} \tag{3.3}$$

$$\mathbf{v}'\mathbf{A} = \lambda\mathbf{v}' \tag{3.4}$$

give the stable stage distribution and reproductive value distributions. It is sometimes convenient to describe population growth by the continuous time growth rate, ln λ, also known as r, the instantaneous rate of increase.

The sensitivity of λ to changes in the entries of $\mathbf{A}$ is given by

$$\partial\lambda/\partial a_{ij} = v_i w_j / < \mathbf{v}, \mathbf{w} > \tag{3.5}$$

where $< \mathbf{v}, \mathbf{w} >$ is the scalar product of $\mathbf{v}$ and $\mathbf{w}$. The proportional sensitivity, or elasticity, of λ is given by

$$e_{ij} = a_{ij}s_{ij}/\lambda. \tag{3.6}$$

In a stochastic matrix model, some elements of **A** vary randomly, so that the model is:

$$\mathbf{n}(t+1) = \mathbf{A}_t\mathbf{n}(t). \tag{3.7}$$

Specifying such a model requires a stochastic model for the elements of $\mathbf{A}_t$: what their probability distributions are, whether they are correlated or vary independently, and how the values at one time are related to those at preceeding times. Although a detailed stochastic model could require much more data than a deterministic one, simple approximations of stochastic processes can be used to simulate natural variability for a variety of demographic factors (Tuljapurkar and Caswell, 1996).

There are now powerful methods available to analyze stochastic models in an analagous fashion to more familiar analyses of deterministic models(Caswell, 1989; Tuljapurkar 1990; Tuljapurkar and Caswell, 1997). Population growth is described by the stochastic growth rate λ_s. It is not calculated as an eigenvalue, but as a long-term average of the growth rates along a trajectory produced by a simulation of Equation 3.7. The stochastic growth rate describes the long-term average of every such realization with probability one, and measures fitness in stochastic life history models (Tuljapurkar 1990). Sensitivities of ln λ_s to changes in matrix elements can also be calculated for the stochastic model, using the stochastic analogs of the stable stage distribution and reproductive value vectors.

Examples of studies using stochastic models include those randomly selecting one of several possible matrices representing differen environmental conditions (Silva et al., 1991; Aberg, 1992; Noda and Nakao, 1996), those generating a series of random matrices by jack-knifing the set of measured vital rates (Gotelli, 1991), and those selecting a single parameter randomly from a specified distribution (Cohen *et al.*, 1983; Nakaoka, 1997). The last approach has the advantage of generating stochasticity in the model from a continuous distibution, which includes a continuous range of values rather than just a few points, and is the approach we chose to take.

For *M. arenaria*, the variability in larval settlement and survival to age one is

vast compared to variability in other matrix elements (Goshima, 1982). Nakaoka (1997) showed that incorporating stochasticity in recruitment into a matrix model had a greater impact on λ_s than did incorporating stochasticity in shell growth rates. Eigenvalue sensitivity to settlement rate has also been shown to be higher than sensitivity to adult survival in *M. arenaria* (Brousseau and Baglivo, 1984). For these reasons, and because we were particularly interested in the process of settlement, we chose to vary only the settlement parameter in this study. Settlement variability was modelled according to a lognormal distribution, which mimics the high degree of variability in settlement of benthic marine invertebrates that is commonly observed (*e.g.* Seed and Brown, 1975; Gaines and Bertness, 1993) better than a normal distribution.

The goal of this paper is to determine the effect of stochastic settlement in a matrix population model, where the settlement is lognormally distributed. We wanted to compare the stochastic model to the results of the deterministic case, which has been previously analyzed for marine invertebrates (*e.g.*, Malinowski and Whitlatch, 1988). This analysis extends the work of Nakaoka (1997) on the marine bivalve *Yoldia notabilis*, who showed that the type of recruitment distribution creating stochasticity in a model, and the choice of parameters to vary greatly influence the population growth rate calculated.

3.2 Methods

3.2.1 Overview

We measured growth and survival of adult *M. arenaria* and gathered other information required for the model, such as population size structure, in Barnstable Harbor, Massachusetts. These data provided all of the information to parameterize the model except for reproductive contributions. Settlement for both the deterministic and stochastic models was estimated from data on *M. arenaria* populations in Japan (Goshima, 1982), because a larger set of data on spatial and temporal variation in

settlement was available in this paper than from our field data. While this combination of data from different sites does not allow us to describe the states of the clam populations in Japan, Massachusetts, or anywhere else, it allows us to explore theoretically the importance of varying settlement against the background of a set of reasonable vital rates. We assume that these parameters are accurate enough to describe in general the population dynamics of *M. arenaria.*

To investigate the role of variability in settlement, we formulated a stochastic model. We chose to include stochastic variation in only larval settlement, holding the rest of the matrix fixed. The analyses cannot actually distinguish whether the variation is caused by changes in fertility , settlement, or larval survival since all are included in calculation of these parameters, but we chose to interpret the results as if all the variation is due to changes in settlement. In the absence of information to specify a more complex temporal pattern, we modelled settlement as varying independently from year to year. This means that we needed to specify only the distribution from which reproductive parameter values were drawn. The deterministic case was modeled as a special case of the stochastic one, in which the variance of the settlement distribution was zero.

3.2.2 Estimation of Adult Growth and Survival

Growth and survival probabilities were measured in a mark-recapture study in Barnstable Harbor, Massachusetts (similar to Weinberg *et al.*, 1996). In March, 1995, sufficient numbers of clams were dug from the intertidal mudflat to select twenty in each of the following shell length size classes: 20–40 mm (class 1) ; 40–49.9 mm (class 2) ; 50–59.9 mm (class 3) ; 60–69.9 mm (class 4) ; and >70 mm (class 5). Size classes were selected to evenly span the sizes present in the population. Although clam growth slows with size, enough large clams grew fast enough that we could measure transitions between the larger size classes. Each clam was measured and marked with an identification number on both valves in indelible pen. Ten clams (two from

each size class) were placed together in each of ten sediment-filled mesh bags (mesh size ca. 20 mm), in their normal orientation with siphon up and at the appropriate depth for their size (about one body length). The bags did not exclude predators, but simply marked the location of the clams and allow for easier sampling. The density of clams within the bags ($80/m^3$)was not greater than natural densities (ca. $400/m^3$). In June, September, and December, the bags were removed, and the clams were sorted from the sediment, counted, and measured. At each sampling time, new clams were collected to replace missing or dead clams, labelled, and mixed with the survivors before placing all clams in new bags as in March 1995. Surviving clams that were re–deployed were assumed to have the same survival and growth rates as newly deployed clams. In March 1996, all clams were removed from the bags, counted, and measured.

3.2.3 Model Formulation

The life cycle graph (Figure 3.1), and the corresponding projection matrix **A** (Figure 3.2), depict the structure of the model and its parameters. The model is stage classified, with birth-pulse reproduction and a pre-breeding census. Stages 1–5 are the size-classes for which growth and survival were measured in the field. Since adult growth and survival data were collected over four contiguous three–month periods, parameters for seasonal projection matrices were calculated. First, transition tables (**T**) were constructed from these data (Table 3.1), then the elements of the seasonal projection matrices, a_{ij}, were calculated from the **T**:

$$a_{ij} = t_{ij}/n_j, \tag{3.8}$$

(Caswell, 1989), where i is the row and j the column of the element in **A** or **T**, and n_j is the number of clams deployed minus the number of missing clams. The seasonal matrices (Table 3.2) were multiplied together to make a single projection matrix with an interval of one year according to Equation 3.2.

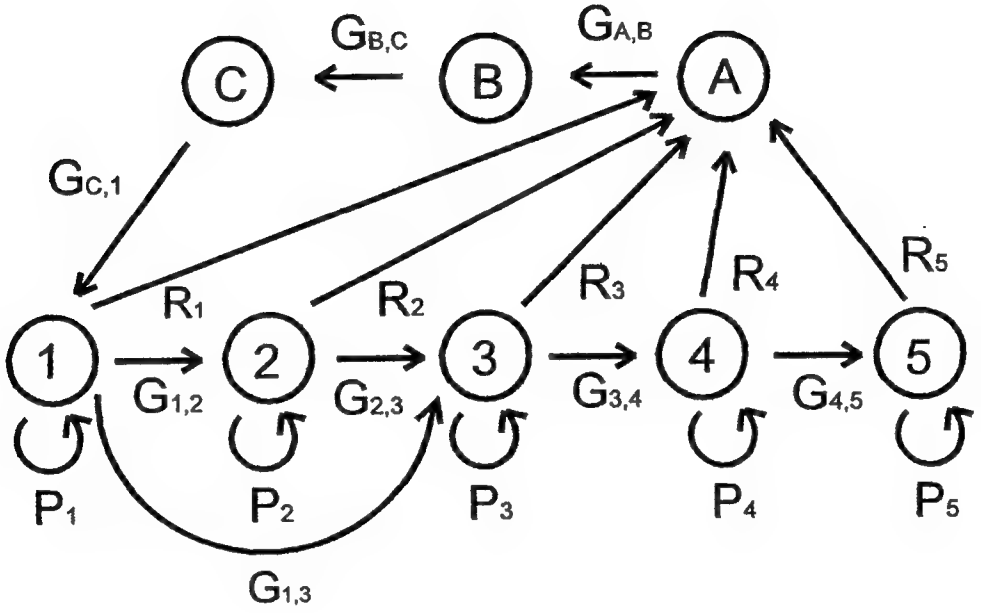

Figure 3.1: The life cycle graph for *M. arenaria*. The circles indicate stages, and the arrows represent these transitions: surviving and growing to a subsequent stage (G_{ij}), surviving and staying in the same stage (P_i), or reproductive contribution to the first stage (R_i). These parameters are denoted R_i, rather than F_i, because they measure *R*ecruitment at the end of the model time step, rather than *F*ertility at the beginning of the time step. Stages A, B, and C are dummy stages, as defined in Model Formulation.

$$\mathbf{A}_s = \begin{pmatrix} & & & R_1 & R_2 & R_3 & R_4 & R_5 \\ G_{A,B} & & & & & & & \\ & G_{B,C} & & & & & & \\ & & G_{C,1} & P_1 & & & & \\ & & & G_{1,2} & P_2 & & & \\ & & & G_{1,3} & G_{2,3} & P_3 & & \\ & & & & & G_{3,4} & P_4 & \\ & & & & & & G_{4,5} & P_5 \end{pmatrix}$$

Figure 3.2: Elements of the seasonal projection matrices, $\mathbf{A}_s$, corresponding to the stage transitions in Figure 3.1. All locations in the matrix where no parameter is shown are zero. In this model, $G_{A,B}$, $G_{B,C}$, and $G_{C,1}$ are always one and are not displayed in subsequent tables of seasonal matrices. The R_i are were calculated according to Equation 3.9and are not displayed either; only P_i and $G_{i,j}$ for i =1–5 are displayed.

Table 3.1: Transition Tables, **T**. Entries in tables, t_{ij}, are the numbers of clams with fate i at time $t+1$ that were in size-class j at time t. Time intervals were three months. Spring was March to June 1995, summer was June to September, fall was September to December, and winter was December 1995 to March 1996. Since the fate of missing clams is unknown, n was used instead of number deployed to calculate parameter values.

	SPRING					FALL				
Fate i at	Class j at t					Class j at t				
$t+1$	1	2	3	4	5	1	2	3	4	5
Class 1	0	0	0	0	0	1	0	0	0	0
Class 2	13	3	0	0	0	3	3	0	0	0
Class 3	2	11	7	0	0	0	3	9	0	0
Class 4	0	0	6	12	0	0	0	0	2	0
Class 5	0	0	0	1	17	0	0	0	0	5
Dead	0	3	4	6	2	5	7	4	12	6
Missing (M)	5	3	3	1	1	11	7	7	6	9
Total (T)	20	20	20	20	20	20	20	20	20	20
n (T-M)	15	17	17	19	19	9	13	13	14	11

	SUMMER					WINTER				
Fate i at	Size j at t					Size j at t				
$t+1$	1	2	3	4	5	1	2	3	4	5
Class 1	0	0	0	0	0	10	0	0	0	0
Class 2	1	1	0	0	0	3	14	0	0	0
Class 3	0	3	0	0	0	1	3	15	0	0
Class 4	0	0	3	3	0	0	0	2	16	0
Class 5	0	0	0	2	5	0	0	0	1	19
Dead	9	13	11	11	14	0	0	2	1	1
Missing (M)	10	3	6	4	1	6	2	1	2	0
Total (T)	20	20	20	20	20	20	19	20	20	20
n (T-M)	10	17	14	16	19	14	17	19	18	20

Table 3.2: Seasonal Projection Matrix Parameter Values. Parameter values were calculated by Equation 3.2.3 from the stage-transition data in Table 3.2.3. Only parameters in the lower right corner of the 8 x 8 matrix shown in Table 3.2 are displayed here: P_i (on the diagonal) and $G_{i,j}$ (on the subdiagonal) for stages 1–5. Since $G_{i,j}$ for stages A, B, and C are all = 1 and R_i vary, they are not shown in these matrices.

SPRING

0	0	0	0	0
0.87	0.18	0	0	0
0.13	0.65	0.41	0	0
0	0	0.35	0.63	0
0	0	0	0.05	0.89

FALL

0.11	0	0	0	0
0.33	0.23	0	0	0
0	0.23	0.69	0	0
0	0	0	0.14	0
0	0	0	0	0.45

SUMMER

0	0	0	0	0
0.1	0.06	0	0	0
0.3	0.18	0	0	0
0	0	0.21	0.19	0
0	0	0	0.1	0.26

WINTER

0.71	0	0	0	0
0.21	0.82	0	0	0
0.07	0.18	0.79	0	0
0	0	0.11	0.89	0
0	0	0	0.06	0.95

Because of the extra information afforded by using seasonal data on growth and survival, we chose to use these data, despite the problem using them created in incorporating the reproductive contribution data. The problem is this: settlement measurement included survival to age one, so the parameter measures reproductive contributions for an annual time step rather than a three-month one. If these parameters were used to quantify transitions from stages 2 through 5 directly to stage 1, this would apply an annual mortality rate to these offspring during their first three months of life, and they would be moved to stage 1 at an age of three months, rather than one year. This discrepancy in timing was resolved by adding dummy stages A, B, and C to the model, as shown in Figure 3.1. In our model, offspring are contributed to stage A according to R_i, which include a year's worth of mortality. But then the juveniles pass through stages B and C to stage one, making each transition with probability one. Therefore, they arrive in stage one at the appropriate survival rate and at the proper time.

3.2.4 Estimation of Reproduction Parameters

To estimate the reproductive parameters in a matrix model, we need to know size-specific fecundity and the survival of those offspring to the next time step. For animals with planktonic larvae, pre–settlement survival is very difficult to estimate, and even estimating post–settlement survival challenging, especially over short time intervals. We allocated the production of observed settling juveniles to size classes in proportion to the reproductive output of that size class (called "anonymous reproduction" in Caswell, 1989). These estimates were adjusted to an annual interval by rough estimates of survival rates from settlement to age one. This method assumes that the population is closed, that is, that larvae spawned by these adults settle back into the same population. The reproductive contributions (R_i) were calculated as: 1) the proportion M_i of population reproductive output contributed by size class i; 2) the number s of recruited juveniles per adult (by area); and 3) the probability S that

settled juveniles will survive to one year of age:

$$R_i = M_i s S. \tag{3.9}$$

To estimate the M_i, eggs per ripe female were counted from histological preparations of gonad samples, using standard stereological methods (Weibel, 1979). Gametogenesis begins in the winter in Cape Cod populations of *M. arenaria*, and spawning occurs throughout the summer from March to September. Samples were taken from five clams per size class in March, June, August, and September 1995. No ripe females in size class two were present in the samples taken. A value was calculated using numbers of eggs from clams collected in Quincy, Massachusetts, which were nearly identicle to those of Barnstable Harbor clams in other size classes. The M_i (Table 3.2.4) were calculated from the mean number, E_i, of eggs per ripe individual in size class i:

$$M_i = \frac{E_i}{\sum_i E_i}. \tag{3.10}$$

Reproduction was incorporated into the model in the summer matrix only. This approach averaged reproductive effort over the spawning season.

An estimate of variability in settlement was obtained from data in Goshima (1982). He provides numbers of just-settled recruits and adults per area, at five sites (less than 400 m apart) over six years. We estimated the ratio of newly settled clams to adult clams (to nearest order of magnitude) from plots of clam density for each time and site (Goshima, 1982: Figure 7). If the plotted value for either young clam density or adult density was zero, we assumed that in twice the area one clam would be found, and so used 0.5 for our calculations. This was done to avoid division by, or taking the log of, zero. The resulting values (Table 3.4) range over several orders of magnitude. These numbers were divided by two to count only female offspring in the model.

The survival probability, S, of the settlers, until the next time step of the model (age one year), was roughly estimated as 0.092. This value is the mean of five years

Table 3.3: Mean numbers of eggs per female in size class i, E_i, sample size, n, the variance of E_i, and proportion of population reproduction from size class i, M_i. Values in parentheses are from Quincy, Massachusetts, population of clams.

Size Class	n	E_i	variance	M_i
1	1	$1.7\text{x}10^6$	0	0.02
2	(1)	$(3.7\text{x}10^6)$	0	0.05
3	4	$6.5\text{x}10^6$	$1.2\text{x}10^{13}$	0.08
4	4	$2.03\text{x}10^7$	$8.7\text{x}10^{13}$	0.25
5	3	$4.77\text{x}10^7$	$1.8\text{x}10^{15}$	0.60

Table 3.4: Numbers of newly-settled clams per adult used to characterize a distribution for the stochastic model, estimated from data in Goshima, 1982.

Site	Year					
	1974	1975	1976	1977	1978	1979
A	8,000	0.04	0.02	4	4	4
C	80,000	0.4	0.02	40	4	40
G	400	0.4	0.4	4	4	4
H	400	0.4	0.002	4000	400	400
E	40	0.04	0.04	0.4	4	40

of data on changes in *M. arenaria* cohort density with time, and was estimated from Figure 9 in Goshima (1982).

3.2.5 Population Structure

Simulations were started with the observed stage distribution in Barnstable Harbor. This distribution, $\mathbf{n}(0)$, was determined from counting and measuring the clams collected in ten cores 30 cm in diameter and 30 cm deep taken near the study site on September 26, 1995. Clams were sorted from the sediment by hand. The population consisted of 3% class 1, 12% class 2, 47% class 3, 28% class 4, and 9% class 5 clams.

3.3 Model Analysis and Results

3.3.1 Deterministic Model

In the deterministic model, the value used for s was the geometric mean of settlement data (Table 3.4), 2.66. The deterministic population growth rate, the dominant eigenvalue of $\mathbf{A}$, was calculated as $\ln \lambda$, and equalled -1.90. This population is expected to decrease (Figure 3.2), but as s is increased, population growth rate will also increase(Figure 3.4).

The equilibrium settlement rate (ESR) was calculated numerically by finding a value of s that gave a $\ln \lambda = 0.00$. (An analytical method for finding ESR for age-classified matrix models is found in Vaughan and Saila, 1976.) The ESR was 211, two orders of magnitude higher than the geometric mean of values measured for *M. arenaria* in Japan (Goshima, 1982).

The stable stage distribution showed that, asymptotically, the population will be dominated by clams in size-class 1 (33%), with the remainder split fairly equally between classes 3, 4, and 5 (about 20% each). This was not the structure of the Barnstable Harbor population at the time that it was sampled, demonstrating that

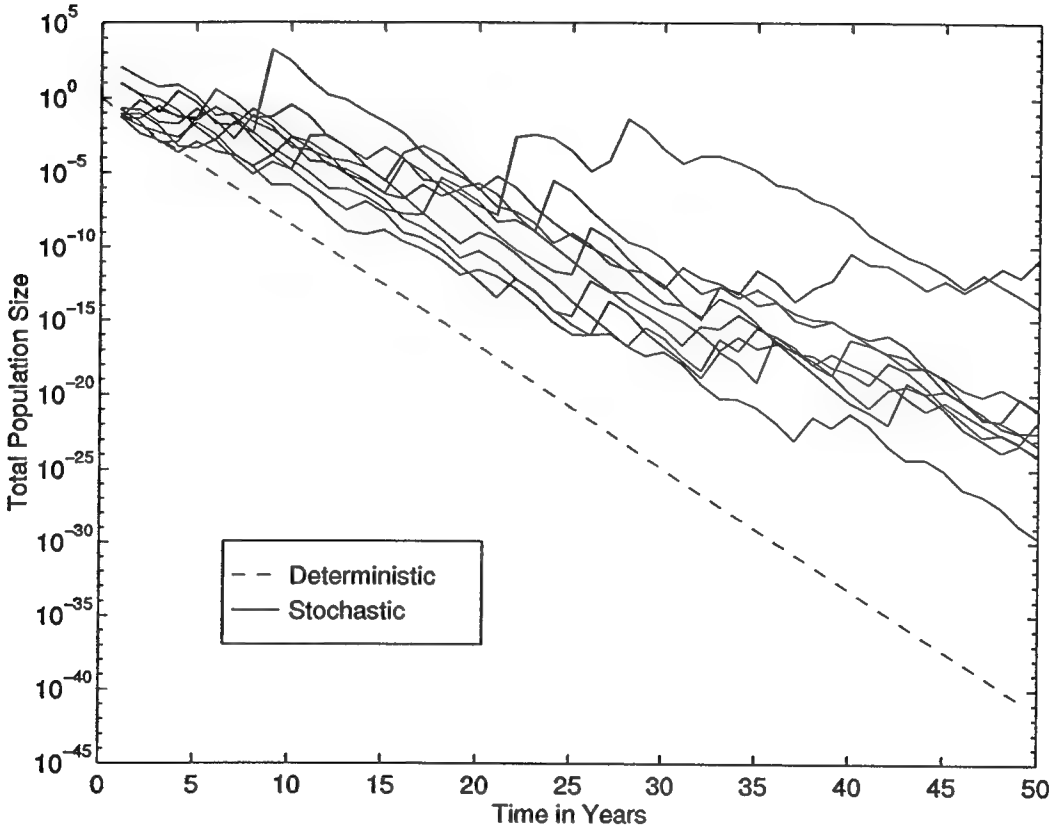

Figure 3.3: Projections of Deterministic and Stochastic Models. Total population size is shown on a logarithmic scale through time in years for the deterministic model (- - -) and ten randomly selected examples of simulations of the stochastic model (—).

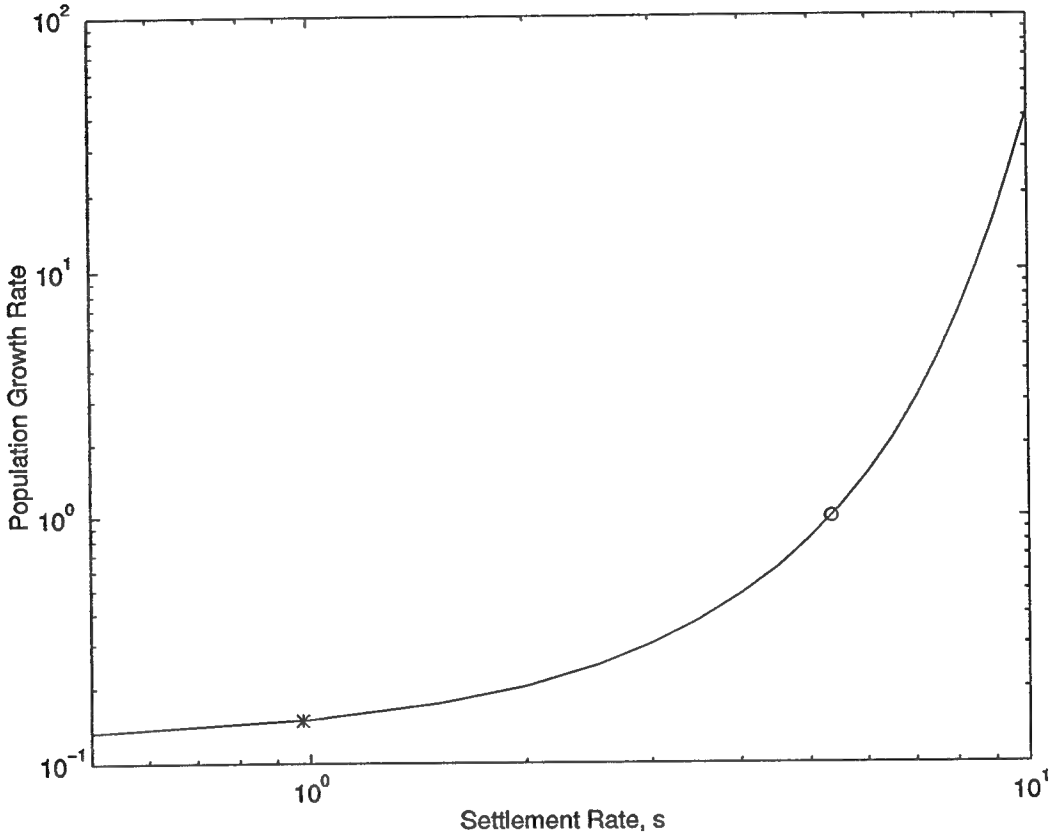

Figure 3.4: Change in deterministic population growth rate, λ, with change in settlement rate, s. The * indicates the value used in the deterministic model to calculate the reported growth rate and the o indicates the value for the ESR, where the population is at equilibrium. The slope of this curve is elasticity of λ to s.

it was not at equilibrium.

Seasonal elasticities were calculated according to the modification of Equation 3.6 for periodic matrices found in Caswell and Trevisan (1994). Elasticities show (Table 3.3.1) that in all seasons, small changes in survival in the largest size class will lead to the largest change in λ of all the parameters. Elasticity to reproduction increases with size, but is low overall. The slope of the log–log plot of changes in λ with change in s (Figure 3.3.1) is the elasticity to s. It increases as s increases.

Sensitivities for the annual matix were calculated as:

$$\frac{1}{\lambda}\frac{\partial\lambda}{\partial a_{ij}} \tag{3.11}$$

for comparison to the stochastic sensitivities. Reproduction in the first size class had the highest sensitivity (Table 3.6), and reproduction in the larger size classes and growth into the largest size class had high sensitivities as well. Sensitivities to transitions from size class two were negligible.

3.3.2 Stochastic Model

The matrix **A** was varied stochastically by changing s at each time step. All other parameters were held constant. Values for s for each simulation were generated randomly (using Matlab), from a lognormal distribution. The lognormal distribution was characterized from a normal distribution with mean and variance of the logarithm of the measured settlement values from Goshima (1982). The anti-logarithm of one of these values was then substituted into the projection matrix at each time. An example of a typical time-series of settlement values generated by this process shows a stereotypical random pattern if it is plotted on a log scale, while on a linear scale , the pattern appears as many years with low settlement and a few years with high settlement (Figure 3.5). Values of s that are higher than the ESR occur 47% of the time. The skewness of the lognormal distribution caused this pattern, which is the important consequence of using it.

Table 3.5: Seasonal elasticity matrices for *Mya arenaria*. Where seasonal matrix elements are zero, elasticities are also zero. Those elements have been replaced in the displayed elasticity matrices with dashes, for clarity.

Spring	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-
	-	-	0.25	-	-	-	-	-
	-	-	-	<0.01	<0.01	-	-	-
	-	-	-	<0.01	0.01	0.04	-	-
	-	-	-	-	-	0.15	0.08	-
	-	-	-	-	-	-	0.01	0.44
Summer	-	-	-	0.01	<0.01	0.02	0.07	0.15
	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-
	-	-	-	0.04	<0.01	-	-	-
	-	-	-	0.21	<0.01	-	-	-
	-	-	-	-	-	0.03	0.03	-
	-	-	-	-	-	-	0.13	0.30
Fall	-	-	-	-	-	-	-	-
	.25	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-
	-	-	-	<0.01	-	-	-	-
	-	-	-	<0.01	0.02	-	-	-
	-	-	-	-	0.02	0.21	-	-
	-	-	-	-	-	-	0.06	-
	-	-	-	-	-	-	-	0.43
Summer	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-
	-	0.25	-	-	-	-	-	-
	-	-	-	<0.01	-	-	-	-
	-	-	-	<0.01	0.01	-	-	-
	-	-	-	<0.01	<0.01	0.19	-	-
	-	-	-	-	-	0.04	0.05	-
	-	-	-	-	-	-	0.01	0.43

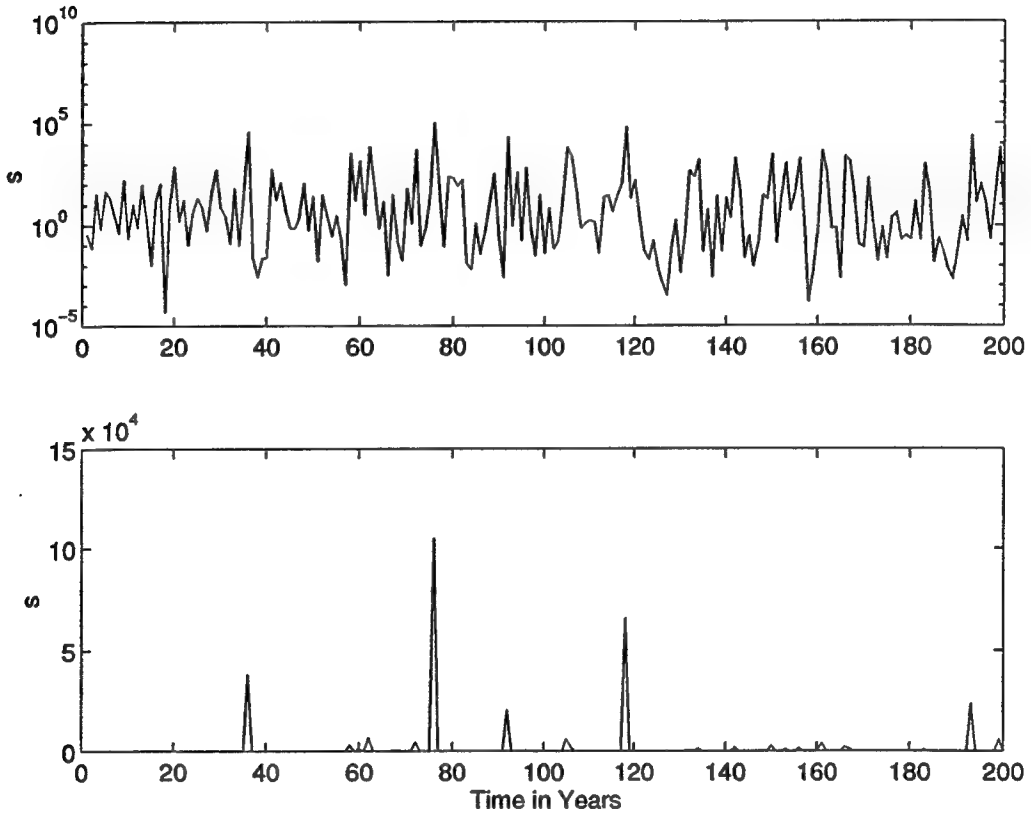

Figure 3.5: Time Series of Stochastic Settlement. An example of a typical time series of randomly generated settlement values plotted on a lognormal scale (upper panel), and on a linear scale (lower panel), showing the type of pattern produced by the stochastic process.

Table 3.6: Sensitivity matrix for annual projection matrix in deterministic model.

0	0	0	7.08	0.16	4.26	4.85	4.36
0	0	0	6.33	0.15	3.80	4.33	3.89
0	0	0	2.15	0.05	1.29	1.48	1.32
0	0	0	1.70	0.04	1.02	1.17	1.04
0	0	0	1.12	0.03	0.68	0.77	0.69
0	0	0	0.57	0.05	0.34	0.39	0.35
0	0	0	2.28	0.05	1.37	1.57	1.41
0	0	0	4.98	0.12	2.99	3.41	3.07

Analysis of the stochastic model consisted of calculating the stochastic growth rate, $\ln \lambda_s$ (Caswell, 1989). First, the one-step growth rates were calculated for each time step of a single population trajectory of length T:

$$\ln \lambda_s(i) = \ln N(i+1) - \ln N(i) \qquad i = 1, ...T-1, \tag{3.12}$$

where N is total population size. Then the mean of the one-step growth rates was calculated:

$$\ln \lambda_s = \frac{1}{T-1} \sum_i \ln \lambda_s(i). \tag{3.13}$$

Finally, the stochastic growth rate was reported as the mean of the $\ln \lambda_s$ from many individual trajectories. In this study, stochastic growth rate was estimated as the mean of ten trajectories, each run for 50,000 time steps with the first 10,000 discarded as transients. For the theoretical population of *M. arenaria* experiencing variable settlement on a lognormal scale, $\ln \lambda_s = -0.95$. Example of trajectories for the stochastic population (Figure 3.3.1) shows that it is projected to decline less rapidly than the deterministic population.

Sensitivities for the stochastic model,

$$\frac{\partial ln\lambda_s}{\partial a_{ij}}, \tag{3.14}$$

were calculated according to the stochastic equivalent of Equation 6:

$$\mathbf{S} = \frac{1}{T}\sum_{t=1}^{T}\frac{\mathbf{V}_t\mathbf{U}'_{t-1}}{\mathbf{V}'_t\mathbf{U}_t\lambda(t)} \tag{3.15}$$

where prime denotes the transpose of a matrix, and $\mathbf{U}_t$ and $\mathbf{V}_t$ are the stochastic analogs of the deterministic stable stage distribution, $\mathbf{w}$, and reproductive value vector, $\mathbf{v}$. These are defined as:

$$\mathbf{U}_{t+1} = \frac{\mathbf{A}_{t+1}\mathbf{U}_t}{\parallel \mathbf{A}_{t+1}\mathbf{U}_t \parallel} \tag{3.16}$$

and

$$\mathbf{V}'_t = \frac{\mathbf{V}'_{t+1}\mathbf{A}_{t+1}}{\parallel \mathbf{V}'_{t+1}\mathbf{A}_{t+1} \parallel}. \tag{3.17}$$

The symbols $\parallel \cdot \parallel$ denote the sum of the vector entries, and the matrices $\mathbf{A}_t$ are the matrices in the sequence generated in the stochastic model (Tuljapurkar, 1990). Stochastic sensitivities (Table 3.7) show the same pattern as deterministic ones, with negligible sensitivity to transitions from stage two, the highest sensitivity to transitions from stage one, and highest sensitivity in each column for reproduction and growing into the largest size classes. The stochastic sensitivities in the upper left of the matrix are about double the deterministic ones, while in the lower right they are almost the same as the deterministic ones. Stochastic sensitivities for transitions from size class one to size classes four and five were more than double those in the deterministic case, indicating that rapid growth to large size would be more important to a population with random settlement than to one with steady settlement.

We were also interested in knowing how strongly our results depended on the estimate of variability in settlement that we used. As a simple measure of the sensitivity of stochastic growth rate to change in the parameters characterizing the lognormal settlement distribution, we calculated the stochastic growth rate for ranges of these

Table 3.7: Sensitivity matrix for annual matrix in stochastic model.

0	0	0	12.73	0.08	2.09	2.55	1.92
0	0	0	11.58	0.08	1.92	2.33	1.76
0	0	0	4.13	0.03	0.69	0.85	0.65
0	0	0	3.50	0.02	0.62	0.76	0.59
0	0	0	2.53	0.02	0.50	0.61	0.48
0	0	0	1.61	0.01	0.38	0.46	0.38
0	0	0	6.01	0.05	1.36	1.66	1.34
0	0	0	13.39	0.12	3.10	3.78	3.06

values. We tested values of the mean of the log of the settlement distribution (holding the variance constant) ranging from -1.5 to 3, and values of the variance of the log of the settlement distribution (holding the mean constant) ranging from 0 to 8, both in increments of 0.5. As the mean and variance of the settlement distribution were increased, the stochastic growth rate increased, but at different rates (Figure 3.6). For population growth rates to reach equilibrium ($\ln \lambda_s = 0$), the variance must be almost doubled over the value used at the *, while the mean must be more than tripled. When the variance of the distribution is equal to zero, the stochastic growth rate equals the deterministic growth rate, as expected.

3.4 Discussion

Incorporating variability, on a lognormal scale, in annual settlement density into a matrix model for *M. arenaria* leads to a dramatic increase in population growth rate compared to that using mean settlement levels. This result suggests that variability

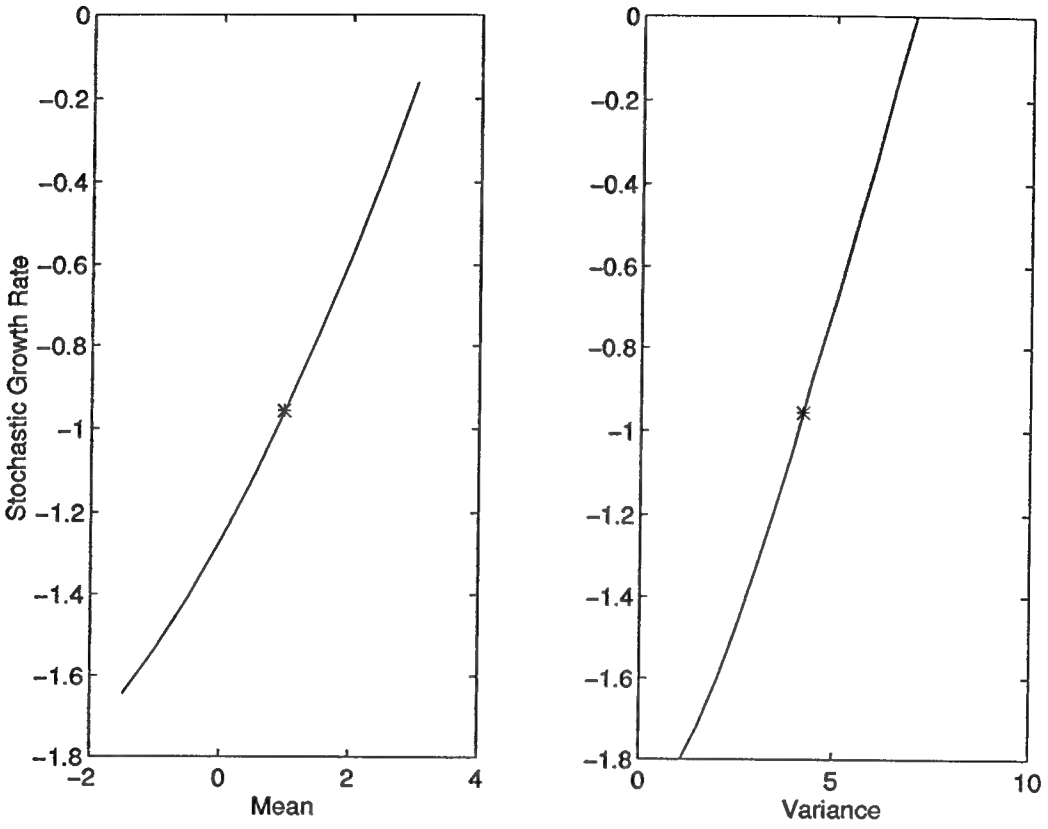

Figure 3.6: Sensitivity of Stochastic Growth Rate to Mean and Variance of Settlement Distribution. The change in stochastic growth rate with change in the parameters specifying the distribution used in generating s values. Means and variances were calculated from the natural logs of the settlement values in Table 3.4. The change in stochastic growth rate with change in the mean of the log of the distribution (left panel), holding the variance constant at the value (4.20) used to calculate the reported λ. The change in stochastic growth rate with change in the variance of the log of the distribution, holding the mean constant at the value (0.98) used to calculate the reported λ. The * indicates the value of the mean (left panel) or variance (right panel) used to calculate the reported λ.

in larval settlement is a critical factor determining population state. Observed large standing stocks of *M. arenaria* may be due to one good year of set, but the population persists because clams live long enough that another good set is likley to occur before they all die. Previous analyses of deterministic models (Brousseau *et al.*, 1982; Malinowski and Whitlatch, 1988) have likely underestimated the potential for growth in *M. arenaria* populations.

These results contrast with those of Gotelli (1991), who concluded that the contribution of variability in recruitment to temporal dynamics of a broadcast-spawning coral was minimal. He created the variability in his model by randomizing twenty-three monthly matrices in series. Variability in recruitment (measured as new colonies appearing in the first size class, each month) ranged over only three orders of magnitude (from 0.00 to 1.22; pers. comm., N. Gotelli), as opposed to the eight orders of magnitude of variability found in our model. This might be due to a shorter planktonic period (3-20 d) for the coral than for *M. arenaria* (14-21 d). The increased amount of variability in our model could easily explain why we found it to be important but Gotelli did not, especially since we also found that increased variability increased stochastic growth rate (Figure 3.6).

Since the model is sensitive to the mean and variance of the distribution used (Figure 3.6), uncertainty as to the parameters describing this distribution would obviously lead to uncertainty in the population growth rate. Since we do not know if the mean and variance of the settlement distribution used here are similar to actual settlement in Barnstable Harbor, there is no reason to conclude that the population there is expected to collapse. In fact, because our results show that the theoretical clam population is decreasing so rapidly, we believe there is some mismatch between growth and survival in Barnstable Harbor and the settlement levels in Japan. The ESR calculated was two orders of magnitude higher than mean settlement in Japan, but that population was not in decline (Goshima, 1982), so clams must have higher survival rates there than in Barnstable, MA. Settlement in Barnstable Harbor mea-

sured in September, 1995 (Ripley and McDowell, in prep.) was 0.43. This means that about 63% of settlement events in our model were larger than measured settlement in Barnstable, suggesting that settlement ranges in Japan may be similar to those in Barnstable Harbor.

Equilibrium settlement rates have been used to estimate larval survival, under the assumption that the population is in equilibrium (Vaughan and Saila, 1976; Brousseau *et al.*, 1982). In this study, the population was not in equilibrium when it was surveyed (the population structure was not the same as the stable stage distribution), and we believe that few field populations of marine bivalves are in equilibrium, making this assumption highly quesitonable. The ESR calculated was much higher than observed settlement, yet the field population of clams in Barnstable have been a productive resource for decades. Given the importance of variation in settlement demonstrated here, we believe that calculation of ESR is of little informational value.

Elasticities calculated here for reproductive parameters in the deterministic case were low, which agree with Gotelli's results. Further, Gotelli (1991) found in a random simulation of 1000 stage-structured matrices that elasticities for survivorship were always larger than those for growth, and that reproductive elasticities were always smallest. However, since they are defined over "small" changes in parameter values, elasticities tell us little about the importance of large changes in the parameters. The results of this study showed that despite small deterministic elasticities, random change in reproductive parameters led to fairly large change in population growth rate. Nakaoka (1997) also found that the recruitment parameters had low elasticities but could cause large changes in λ when they were made stochastic.

Variation in growth rates or survival, certainly plays a role in population processes of *M. arenaria* which we did not address in this study. However, variability in recruitment was shown to play a larger role in determining population growth than variation in shell growth rates by Nakaoka (1997). Indeed, since growth and survival parameters are probabilities and must be between zero and one, it is always possible

for the fecundity parameters to vary much more widely. Growth rates are also more likely to vary over much smaller ranges, which would cause less dramatic changes in population growth rates. It is important to select the appropriate vital rates to vary in a model to answer speciific questions about their role in population processes (Noda and Nakao, 1996; Nakaoka, 1997), and here we chose to focus on settlement.

The settlement data used here are lognormally distributed (according to a normal probability plot; not shown), which means that the distribution is skewed, with few large values and many more small ones. Other marine invertebrate recruitment data sets have also shown lognormal trends. The distribution Nakaoka (1997) used was lognormal, estimated from a large data set (ca. 20 years) of recruitment in *Yoldia notabilis*, a bivalve which is similar in life history to *M. arenaria*. Noda and Nakao (1996) observed massive recruitment for a species of marine gastropod once in every eight years, with little or none in between, also suggesting a lognormal pattern. Recruitment patterns for marine invertebrates have repeatedly been shown to have this kind of pattern (*e.g.* Coe, 1956; Loosanoff, 1964; Caffey, 1985), so our results may be broadly applicable. Further research is needed in characterizing recruitment dynamics of intertidal organisms so that it is possible to describe year-to-year and spatial variability more completely. It would also be interesting to investigate density-dependence of recruitment, which might damp the changes in population size due to changes in settlement generated in this density-independent model. Characterizing how recruitment varies with different developmental modes will also be crucial to understanding marine invertebrate population dynamics.

What is the role of variability in settlement in the life history of marine invertebrates? Results here suggest that the advantage of broadcasting larvae may not be solely in greater dispersal (Palmer and Strathmann, 1981; Strathmann and Strathmann, 1982), but also in periodic large recruitment successes. For animals with a life span long enough to sustain populations through several years with no settlement, broadcast spawning is a gamble with potentially big payoffs. Alternatively, the low

parental investment of energy into planktonic larvae, which leads to variability in settlement, may have led to the possibility of long life span. In either case, adult life span and variable recruitment are linked.

3.5 Summary

1. Equilibrium settlement rates provide little, if any, information on settlement impact on population structure.

2. Variability in settlement is apparently a gamble worth taking for *Mya arenaria* populations. This conclusion is expected to hold true for other organisms with high fecundity, uncertain recruitment, and relatively long life spans.

3. While deterministic models may be useful in comparing populations to one another, stochastic models present a much different picture of population processes for organisms with highly variable vital rates, if that variability can be characterized.

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Chapter 4

The interaction of chronic contaminant exposure and ecological factors in population processes of an infaunal clam

4.1 Introduction

The physiological effects of lipophilic organic contaminants on marine bivalve molluscs have been examined extensively during the past decade. The majority of the studies have been conducted on the blue mussel *Mytilus edulis* (*e.g.*, Bayne *et al.*, 1985; Bayne *et al.*, 1988) with an effort to integrate responses over several levels of biological hierarchy and to examine responses linked to specific classes of contaminants. The general results of this research are that tissue burdens of lipophilic organic compounds may interfere with normal metabolic processes influencing growth, development, and reproduction (Capuzzo *et al.*, 1988). Exposure to contaminants is known to impair physiological mechanisms (Capuzzo and Sasner, 1977; Gilfillan *et al.*, 1977; Widdows, 1985), co–occur with histopathological disorders (Moore, 1988; Lowe, 1988), and

cause loss of reproductive potential (Berthou *et al.*, 1987; Neff and Haensly, 1982). Recent work has extended this approach to other species of bivalve molluscs, such as the subtropical turkey wing mussel, *Arca zebra* (Addison and Clarke, 1990; Widdows *et al.*, 1990) and the soft shell clam, *Mya arenaria* (Leavitt *et al.*, 1990; Weinberg *et al.*, 1997; McDowell Capuzzo *et al.*, in prep.).

The soft-shell clam, *Mya arenaria*, is common and commercially important in temperate mudflats along the eastern US. It lives at high densities at both clean and contaminated sites, such as New Bedford Harbor, MA, and the Boston Harbor, MA, area. Even in areas where *Mytilus edulis* has oocyte atresion to the point that they are not reproducing, *M. arenaria* appears to be reproducing normally (McDowell Capuzzo and Leavitt, 1995). Gardner and Pruell (1988), however, found significant histopathological lesions in soft shell clams at selected contaminated sites in Quincy Bay including gill inflammation, atypical cell hyperplasia in gill and kidney, hyperparasitism with rickettsia in digestive ducts/tubules, and general parasitism. Similar results were found by Moore *et al.* (1996).

Changes in population structure and dynamics are likely results of alterations to reproductive and developmental potential, which are expected results of chronic exposure to chemical contaminants. Alterations in bioenergetics linked with observations of reduced fecundity and viability of larvae, abnormalities in gamete and embryological development, and reduced reproductive success provide a strong empirical basis for examination of population responses. Koojiman and Metz (1984) suggested that such sublethal effects of contaminant exposure should be interpreted in light of the survival probabilities and reproductive success of populations, bridging the gap between individual and population responses. Although a wide range of sublethal stress indices have been proposed for evaluation of chronic responses of organisms to contaminants, few have been linked to the survival potential of the individual organism or the reproductive potential of the population.

From the known deleterious effects of contaminant exposure on bivalves, we would

expect *M. arenaria* living at contaminated sites to be unhealthy. However, we find dense populations of this clam at contaminated sites. The observed population tolerance to chemical stress may be due to one or more of the following reasons: 1) healthy larvae spawned at clean sites recruiting to contaminated sites and subsidizing populations; 2) reductions in survival, growth, or reproduction are not sufficient to suppress population growth; 3) predators (including humans) are less tolerant than clams to chemical contaminant exposure; 4) organic enrichment at contaminated sites provides nutrition for clams; and 5) adaptation to chemical contaminant exposure. As a first step in understanding the differences in populations found at contaminated and uncontaminated sites, we assessed (2) by measuring clam growth, survival, fecunditity, and recruitment at five sites across a gradient in contaminant concentrations. Using a matrix population model, vital rates were integrated to evaluate the population level effects of differences in individual physiological parameters.

The matrix population model can be thought of as an analytical tool that combines vital rates of individuals into information about the population as a whole. If we assume that potential biochemical, cellular, and physiological changes associated with contaminant stress are manifested as changes at the organismal level, namely in fecundity, survival, and growth, we can say that the matrix model integrates these factors and addresses their combined effect at the population level.

To construct a matrix population model, the population is divided into categories that correspond to changes in vital rates over the life span of the animal. In this case, size-classes were used, since for *M. arenaria*, important life history traits such as predation rates (Blundon and Kennedy, 1982) and fecundity (Brousseau, 1978) are size-specific, and because size is more easily measured than age. The set of linear equations that describe the proportion of clams that move between these categories in a given time step, are written, in matrix notation, as:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t). \tag{4.1}$$

The vectors $\mathbf{n}$ are size-class frequency distributions and $\mathbf{A}$ is the projection matrix.

Each element, a_{ij} (the matrix element in the ith row and jth column of $\mathbf{A}$), represents contributions from class j to class i over one time step. Elements on the diagonal of $\mathbf{A}$ represent survival and stasis, and are noted P_i. Elements on the subdiagonal represent survival and growth between size-classes, and are noted $G_{i,j}$. Contributions to the smallest size class via reproduction appear in the first row of the matrix, and are noted here as R_i.

Analysis of the model includes calculation of the dominant eigenvalue of $\mathbf{A}$, λ, which is the asymptotic population growth rate and a measure of mean fitness of individuals in the population (Caswell, 1989). Elasticities are the proportional sensitivities of λ to each matrix element, and are the relative contributions of the matrix elements to fitness. These contributions can be compared between populations by doing a life table response experiment (LTRE) decomposition (Caswell, 1996). By treating the whole life table as the response variable, one can calculate where in the life table the differences in λ between populations are found (Caswell, 1989). Elasticity analysis and LTRE decompositions are powerful methods to evaluate what parts of the life cycle have the most impact on population processes (*e.g.* Levin *et al.*, 1996, and other work cited in Caswell, 1996).

4.2 Methods

4.2.1 Study Sites

Based on surveys of lipophilic organic contaminant concentrations and histopathological conditions of soft shell clam populations, we selected five sites from those previously studied in Boston Harbor and Massachusetts Bay (Moore *et al.*, 1996; Shea and Seavey, 1994). Three contaminated sites around Boston—Saugus River, Fort Point Channel, and Neponset River—and two reference sites about 100 km away from Boston on Cape Cod—Wellfleet and Barnstable Harbors—were selected (Figure 4.1). On the basis of sedimentary PAH concentrations, these sites reflect a gradient of

contamination and observed histopathological effects in soft shell clam populations. Sites were similar in sediment type (sandy mud).

Sediment and clam tissue contaminant concentrations (Table 4.1) were evaluated during the sampling for this study (McDowell and Shea, 1996). Clams for chemical analyses were collected with the clams used for analyses described in this study, and sediment samples for chemical analysis were taken at the locations where clams were deployed in the mark–recapture study. Low levels of contaminants are present even at Barnstable and Wellfleet Harbors, the Neponset site is moderately contaminated, and the Saugus River and Fort Point Channel sites are highly contaminated. The differences between sediment and clam concentrations of these chemicals reflects differences in bioavailablity and bioaccumulation of specific compounds, and perhaps saturation threshholds, as discussed in McDowell and Shea (1996).

4.2.2 Adult Growth and Survival

Growth and survival probabilities were measured in a mark-recapture study (similar to Weinberg *et al.*, 1996) at each site. Measurements were made separately during four periods of time over the year, as growth and survival of *M. arenaria* are known to change seasonally (Brousseau, 1978, 1979). In March 1995, sufficient numbers of clams were dug from the intertidal mudflat to select twenty in each of the following shell length size classes: 20–40 mm (class 1) ; 40–49.9 mm (class 2) ; 50–59.9 mm (class 3) ; 60–69.9 mm (class 4) ; and >70 mm (class 5). Size classes were selected to include all sizes present in the populations. Although clam growth slows with size, clams were expected to grow enough to measure transitions between larger size–classes.

Each clam was measured and marked with an identification number on both valves in indelible ink. At this time, clams at each site were numbered from one to one hundred. Ten clams (two from each size class) were placed into separate holes poked in each of ten sediment-filled mesh bags (mesh size ca. 20 mm) buried so that the surface of the sediment that they contained was flush with the surrounding sediment,

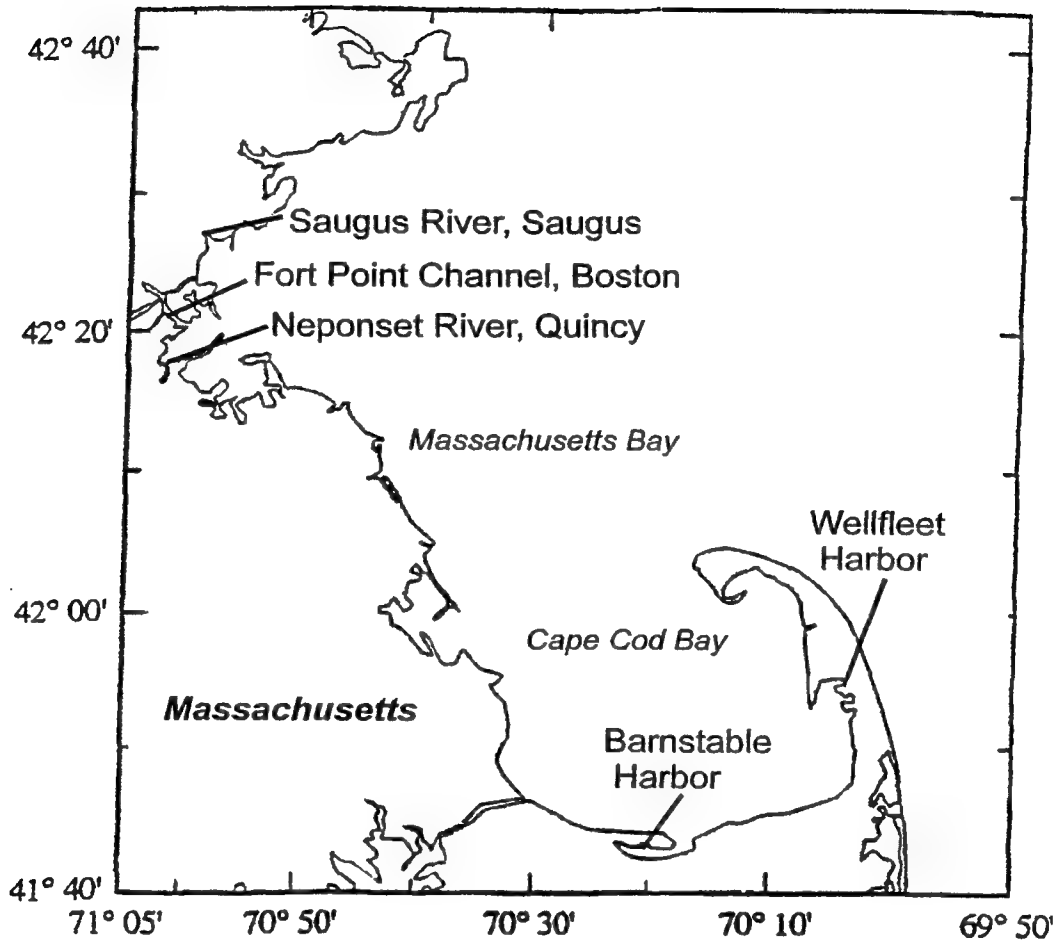

Figure 4.1: Map of study sites in Massachusetts, USA. Latitudes are north, longitudes are west.

Table 4.1: Sediment and Clam Tissue Contaminant Concentrations (ng/g dry weight). Polycyclic aromatic hydrocarbons (PAH), polychlorinated biphenyls (PCB), dioxins (DDT), and linear alkyl benzenes (LAB) in sediment samples and in clam tissues. Values are the means of two samples each of sediments and clams collected in March, 1995 (from McDowell and Shea, 1996). Clams were selected randomly from the population sampled for the mark–recapture study. Sediments were collected no farther than 1 m from locations where clams were deployed in the mark–recapture study.

Site	Total PAH		Total PCB		Total DDT		Total LAB	
	sed.	clams	sed.	clams	sed.	clams	sed.	clams
Barnstable H.	352	300	0.5	11.5	0.2	9.1	7	80
Wellfleet H.	102	367	<0.1	14.7	0.2	0.4	10	360
Neponset R.	1,450	1,900	5.4	130.5	2.0	14.4	31	1,680
Saugus R.	18,342	5,110	12.8	91.1	5.1	20.6	65	910
Fort Point C.	66,121	7,370	34.8	56.7	26.8	14.4	925	8,400

in their normal orientation with siphon up and at the appropriate depth for their size (about one body length). Bags were located near the center of the region of the mud flats exposed at mean low water. The bags did not exclude predators, but simply marked the location of the clams and allowed for easier recovery. The density of clams within the bags ($470/m^3$)was about half the mean of natural densities at the sites ($820/m^3$). In June, September, and December, the bags were removed, the clams were sorted from the sediment, and growth and mortality rates determined by noting the numbers and valve lengths of the clams found alive or dead. At each sampling time, new clams were collected to replace missing or dead clams, labelled, and mixed with the survivors before placing all clams in new bags as in March 1995. New numbers were used to label the clams at each time, so that they were not confused with survivors from the previous time period (*i.e.* clams first deployed in June were numbered starting with 101; those first deployed in September were numbered starting with 200; and those first deployed in December were numbered starting with 300). Surviving clams that were re–deployed were assumed to have the same survival and growth rates as newly deployed clams. In March 1996, all clams were removed from the bags, counted, and measured.

An additional set of ten bags was deployed at each site in March 1995 and not removed until March 1996, to assess the effect of regularly disturbing clams in the three-month deployments.

There were clams missing from the bags on most sampling dates, and on occasion entire bags were missing. All of the winter bags in Saugus were missing in March 1996. To obtain data on winter growth and survival in Saugus, another set of bags was deployed at this site during the next year. These bags were in place from January to April 1997. Some difference in growth and survival between years is expected, so these data were not the best to use to compare to the other sites in a different year, but they are the only data available.

Missing clams were probably either washed out of bags after they had died, or

were removed by predators. We found some of the valves near the bags on the surface of the sediment, so some of the missing clams were clearly dead. They could not all be dead, however, because when we assumed that they were dead, the model results predicted that the probability of finding large clams would be much smaller than the actual probability of finding them in the field. Due to this uncertainty over the fate of missing clams, we based calculation of matrix parameters only on the clams that were found. This assumes that the proportion of live clams is the same for the missing clams as for the ones we found. If this assumption is wrong, parameter estimates are either low or high, depending on whether a smaller or larger proportion of the missing clams are alive than was the case for the clams we found.

Matrix elements P_i and $G_{i,j}$ for i, j = 1–5 were calculated for each size class, season, and site from the field data. The stasis parameters, P_i, and were calculated as the number of clams in size class i at season t that were found alive and in size class i at season $t+1$, divided by the total number of clams in size class i at season t that were found (alive or dead) at season $t+1$. The growth parameters, $G_{i,j}$, were calculated as the number of clams at size class i at season t that were found alive in size class j at $t+1$, divided by the total number of clams in size class i at season t that were found (alive or dead) at season $t+1$.

4.2.3 Reproductive Cycle and Fecundity

To document the annual reproductive cycle and measure fecundity, five clams from each of the five size classes selected for growth and survival measurements were collected from the intertidal area at each site in March, June, August, Septmeber, and December. The clams were brought into the laboratory where they were measured, dissected, and the digestive gland–gonad (DG) complex was weighed. Aliquots of gonad tissue were cut from the DG complex, weighed, and fixed in 10% formalin in 0.45 μm filtered seawater. Samples were embedded in paraffin, sliced into ca. 8 μm sections, mounted on slides, and stained with hematoxylin–eosin (Humason, 1972).

Prepared slides from each clam were examined for gender and reproductive condition according to the definitions of indifferent, early developing, late developing, ripe, spawning, and spent gonadal condition in *Mya arenaria* (Coe and Turner, 1938; Ropes and Stickney, 1965). To estimate fecundity, eggs were counted from prepared slides for female clams in a late developing or ripe stage, using standard stereological techniques (Weibel, 1979) that have been used previously to estimate fecundity of *M. arenaria* (*e.g.* Brousseau, 1978). Estimates were made from examination of slides under a light microscope, using a digitizing pad, Sigma Scan software, and a camera lucida to count and measure eggs. The mean number of nucleated eggs per unit area was calculated for one gonad section per clam, based on counts of nucleated eggs in 10 non-overlapping 10x10 unit retucule grids. The mean oocyte diameter and nuclear diameter of 25 nucleated eggs per gonad section were measured. The number of eggs per unit volume of gonad were calculated by converting grid units to area (mm^2), dividing by the number of grid squares (100), and dividing by mean nuclear diameter. The total number of eggs per gonad was calculated based on the total volume of the DG complex (calculated from data on weight-to-volume ratio of the DG complex), the total percent of gonadal tissue within the digestive gland-gonad complex (D. Leavitt, unpublished data), and the number of eggs per volume of gonadal tissue.

4.2.4 Recruitment and Population Structure

Reproductive contributions in matrix models (the first row of **A**) are usually denoted F_i and are estimated as fecundity multiplied by the probablity that offspring survive to the next model time step. This method is problematic for soft shell clams and other marine invertebrates that have planktonic larvae, because we know so little about transport patterns and survival during both the planktonic period and early post-settlement life. One can estimate fecundity from histological sections of gonads, but it is difficult to estimate larval survival. Matrix models have actually been used to estimate larval survival (Brousseau *et al.*, 1982; Vaughan and Saila, 1976), but

these models cannot also be used to obtain a population growth rate because it is necessary to assign a value to λ to calculate larval survival.

In this study, we defined recruits as clams that had settled and survived at the study site to age one year. The ratio of recruits to adults, r, is used in the model as the basis of the reproductive contribution parameter. This method avoids the problem of not being able to quantify larval survival because it matches the time scale over which we can keep track of young clams. The parameter used here is denoted R_i to emphasize this different method of estimation. R_i are calculated as:

$$R_i = 0.5 r M_i \tag{4.2}$$

where M_i is the proportion of population reproductive output contributed by size class i. This was calculated as the mean fecundity of females in class i, divided by the sum of mean fecundities over all size classes. Using this factor maintains the population structure of the model, but assumes that the population is closed with respect to recruitment. This method also assumes that offspring from different sizes of clams have equal survival probabilities, and that the population that actually spawned the settling juveniles (not necessarily the one at the study site) has the same size structure as the study population. Recruitment is multiplied by 0.5 to count only females, assuming a 1:1 sex ratio (Brousseau, 1978).

To measure r, we had to be able to identify one-year (365 day) old clams. We estimated the size of one year old clams by measuring more than 200 clams, collected in August 1995, from Barnstable Harbor, known to have set on a flat with no other clams on it about one year prior to sampling (pers. com., Tom Marcotti, Barnstable Shellfish Biologist). These clams ranged in size from 17 to 40 mm, with a mean of 26.49 $\pm$ 3.98. The upper limit of this range fell so closely to the size class cut-off of 40 mm that clams less than that size were assumed to be one year old or less. This assumption doubtless underestimates recruitment in Barnstable Harbor, since clams that settled in the spring will be larger than this size, but may overestimate recruitment at the other sites if those clams grow more slowly.

Recruitment and clam densitites in the field were estimated at each site in ten replicate 30 cm–diameter by 30 cm–deep cores by measuring and counting the clams. Cores were taken haphazardly in areas where clams were present, as evidenced by their siphon holes at the sediment surface. Cores were taken in September 1995, about one year from the last spawning event of the previous year, and again in June 1996. Clams were picked from the sediment by hand, measured, and counted. The ratio of clams less than 40 mm to those larger than 40 mm (r) was calculated for each site based on total numbers measured in 1995.

4.2.5 Data Analysis

The sites we studied differ in many factors besides contaminant concentrations, so they cannot be treated as representing individual contaminant levels. Hypotheses about differences between clams at uncontaminated and contaminated sites were tested by treating the two least contaminated sites, Barnstable and Wellfleet, as replicates of the "clean" condition, and the two most contaminated sites, Fort Point Channel and Saugus, as replicates of the "contaminated" condition. Everywhere that these comparisons are made, the words "clean" and "contaminated" appear in quotation marks to alert the reader. Hypotheses concerning recruitment, growth, fecundity, and survival were tested in this way. Note that these are not interpreted as tests for the effects of contaminants on clams, merely as tests for differences between clams living at sites where there are contaminants present and those where contaminants are not present.

Where statistical tests were done using data based on size classes, the original size classes were used, not the revised classes (1' to 5') used to calculate matrix paramters. All means are reported $\pm$ one standard error. ANOVAs and t–tests were performed using the SPSS statistical package (v. 6.1, SPSS Inc., Chicago, IL), and log–linear anlyses were performed using Systat (v. 7.0, SPSS Inc. Chicago, IL).

4.2.6 Model Formulation and Analysis

Because of the extra information afforded by using seasonal data on growth and survival, we chose to use these data, despite the disparity in time step length between these data and reproductive contribution data. The problem is this: recruitment was measured as settlement and survival to age one, so the parameter is over an annual time step rather than a three-month step, as in the case of growth and survival data. If these parameters were used to quantify transitions from stages 2 through 5 directly to stage 1, this would apply an annual mortality rate to these offspring during their first three months of life, and they would be moved to stage 1 at an age of three months, rather than one year. This discrepancy in timing was resolved by adding dummy stages A, B, and C to the model (Figure 4.2). In our model, offspring are contributed to stage A according to R_i, which include a year's worth of mortality. But then the juveniles pass through stages B and C to stage one, making each transition with probability one. Therefore, they arrive in stage one at the appropriate survival rate and at the proper time.

Parameters for seasonal matrices at each site were calculated as described above. Seasonal matrices, $\mathbf{A}_s$, were multiplied together in sequence ($\mathbf{A}_{winter}$ x $\mathbf{A}_{fall}$ x $\mathbf{A}_{summer}$ x $\mathbf{A}_{spring}$) to yield an annual projection matrix, $\mathbf{A}$, for each site. As it turned out, larger clams were growing too slowly to grow between size classes at all sites but Barnstable Harbor. This caused the annual matrices at these sites to be reducible, that is, it was not possible for clams to move into some stages. Irreducibility is required for all of the properties of eigenvalues and eignevectors described by the Perron-Frobenius theorem, and the subsequent analysis of the model, to hold (Caswell, 1989).

To remedy this problem, the data were regrouped into a set of size classes which were narrower in width as the clams got larger: 20–40 mm (class 1'); 40-54.9 mm (class 2'); 55-59.9 mm (class 3'); 60-64.9 mm (class 4'); and >65 mm (class 5'). This change caused there to be fewer clams starting in size classes 3' and 4' than in 3 and 4. Although the new size classes did not make the Wellfleet, Saugus, Neponset, or

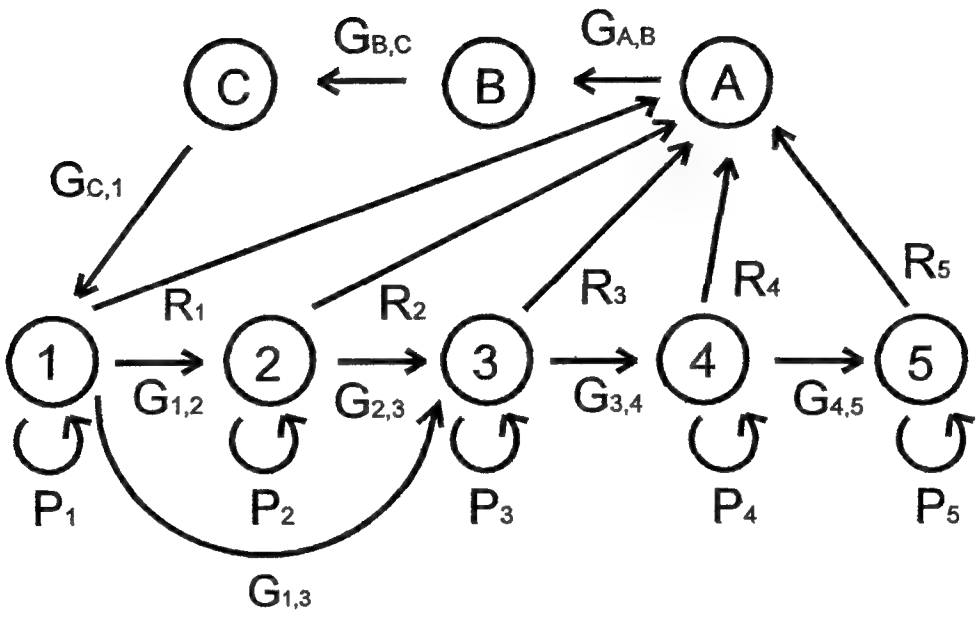

Figure 4.2: Life Cycle Diagram for *Mya arenaria*. The circles indicate stages, and the arrows represent these transitions: surviving and growing to a subsequent stage (G_{ij}), surviving and staying in the same stage (P_i), or reproductive contribution to the first stage (R_i). Stages A, B, and C are dummy stages, designed to align the timing of recruitment parameters with growth and survival parameters. The corresponding seasonal projection matrix is found in Table 4.2.

Table 4.2: Elements of the seasonal projection matrices, $\mathbf{A}_s$, corresponding to the stage transitions in Figure 4.2.6. All locations in the matrix where no parameter is shown are zero. In this model, $G_{A,B}$, $G_{B,C}$, and $G_{C,1}$ are always one and are not displayed in subsequent tables of seasonal matrices. Since the R_i only occurr in the spring or summer matrices (depending on site) and are calculated according to Equation 4.2, they are not displayed in subsequent seasonal matrix tables either; only P_i and $G_{i,j}$ for i=1–5 are displayed.

$$\mathbf{A}_s = \begin{pmatrix} & & & R_1 & R_2 & R_3 & R_4 & R_5 \\ G_{A,B} & & & & & & & \\ & G_{B,C} & & & & & & \\ & & G_{C,1} & P_1 & & & & \\ & & & G_{1,2} & P_2 & & & \\ & & & G_{1,3} & G_{2,3} & P_3 & & \\ & & & & & G_{3,4} & P_4 & \\ & & & & & & G_{4,5} & P_5 \end{pmatrix}$$

Fort Point Channel matrices reducibile, it reduced the number of changes required. The Wellfleet Harbor annual matrix was made reducible by replacing the zero-valued $G_{1,2}$ parameter in the summer matrix with 0.01(an arbitrarily chosen small value). Saugus and Neponset annual matrices were made reducible by adding 0.01 to the zero-valued $G_{3,4}$ parameter in the summer matrix. Only two clams were found alive at Fort Point Channel in the fall, so zero-valued parameters P_3, P_4, $G_{1,2}$, $G_{3,4}$, and $G_{4,5}$ had to be replaced with 0.01 to make the annual matrix reducible.

Population growth rates, and elasticities for periodic matrices were calculated according to Caswell (1989) and Caswell and Trevisan (1994).

Since recruitment rates are known to be variable (Goshima, 1982), some investigation of how large changes (rather than the small ones implicit in analytical sensitivity analysis) in the recruitment parameter might effect the population growth rate was desirable. This was tested numerically by calculating population growth rates using the highest and lowest vaues of recruitment measured for any site, to compare with population growth rates calculated with the measured site-specific recruitment rates.

We calculated an LTRE decomposition matrix to determine which matrix parameters caused the difference between λ values at the "clean" and "contaminated" sites. The difference in population growth rate, $\Delta\lambda$, between the annual matrix $\mathbf{A}^{FS}$, calculated from the means of the seasonal matrices from Fort Point Channel and Saugus River, and the matrix $\mathbf{A}^{BW}$, the annual matrix calculated from the means of the seasonal matrices from Barnstable and Wellfleet Harbors was approximated by:

$$\Delta\lambda \approx \sum_{s}\sum_{i,j}(b_{ij(s)}^{FS} - b_{ij(s)}^{BW})\frac{\partial\lambda^{M}}{\partial b_{ij(s)}}\,|_{M},\ \textit{where}\ M = \frac{\mathbf{A}^{FS} + \mathbf{A}^{BW}}{2} \qquad (4.3)$$

where s are seasons, b_{ij} are elements of the seasonal matrices for "clean" and "contaminated" sites, and $\mathbf{A}$ are annual matrices for these sites. Essentially, the periodic sensitivities of λ to the mean of clean and contaminated matrices is multiplied element-by-element by the element-by-element difference between the two matrices (Caswell, 1989), for each season.

4.3 Results

4.3.1 Adult Growth and Survival

It is likely that survival and growth of clams in the field experiment were compromised by the stress caused by digging them up, drying and handling them, and replacing them in the sediment. An assessment of the impact of handling on clam growth can be obtained from comparing growth rates of clams in the one–year study to the clams in the three–month studies. For clams in the three-month bags, growth over the year was calculated as difference in length between March 1995 and 1996. The majority of clams surviving the year in the one–year bags came from Saugus and Neponset (69/71), while in the three–month bags, the majority (11/15) came from Neponset. As no meaningful comparison could be made between sites, all sites were pooled. Differences in growth between inter–sampling periods was tested with size–class in a 2–way ANOVA (Table 4.3). No difference was detected between growth in one year ($\overline{X} = 4.44 \pm 0.75$ mm) and the four three–month ($\overline{X} = 4.13 \pm 2.0$ mm) treatments p=0.67).

More clams were found at the end of the one-year treatments than at the end of the fourth three-month ones. More clams may have washed out of the three-month bags since the sediments in the bags left undisturbed for a year were more compact and stable than those which had been reworked during sampling three times. Growth rates did not differ between the lengths of time bags were deployed, and since clams were treated the same at each site, we feel that handling stress is not an important factor to consider in making comparisons between these sites.

Growth rates were only calculated for clams found alive. Differences in clam growth between "clean" and "contaminated" sites was tested against size class and season by 3–way ANOVA (Table 4.4). All three factors were highly significant, as well as all interactions except site–by–size class. Mean growth over all seasons and size classes was 1.9 ± 0.15 mm/3 months for clams at the "clean" site and 0.42 ± 0.11

Table 4.3: ANOVA table for growth in one–year and three–month bags. Source of variation (Source) is explained by the sum of squares (SS), degrees of freedom (*df*), mean square (MS), F statistic (F), and significance (p). "Timing" is the variable for length of time bags were deployed.

Source	SS	*df*	MS	F	p
Main Effects	1206.1	5	241.2	10.7	<0.001
Timing	4.2	1	4.2	0.2	0.67
Size Class	1205.1	4	301.4	13.3	<0.001
Timing x Size Class	31.0	4	7.8	0.3	0.85
Explained	1882.4	9	209.2	9.3	<0.001
Residual	1717.8	76	22.6		
Total	3600.2	85	42.4		

mm/3 months at the "contaminated" site. Further, growth was higher at the "clean" site any way means were compared. Clams in larger size classes grew much more slowly than smaller clams (Figure 4.3).

Affects of site, season, and size-class on survival were compared by log–linear analysis, since survival data are frequencies. Number of clams in each size class at time t that were dead or alive at time $t+1$ were tallied. Under the null hypothesis of fate (being dead or alive) being dependent on initial state and independent of site and season, models including state and fate but with different combinations of site, season, and interaction terms were compared. Significance was tested on the difference of G^2 and degrees of freedom between models which were identical except for the term(s) in question (Caswell, 1989). Models are hierarchical and are specified here by the highest level interaction terms that they include. Model comparisons (Table 4.5) showed highly significant site (FT, SFT) and season (FL, SFL) effects. These effects were still highly significant when tested on models that included the other factor,

Table 4.4: ANOVA Table for growth rates. Source of variation (Source) is explained by the sum of squares (SS), degrees of freedom (*df*), mean square (MS), F statistic (F), and significance (p).

Source	SS	*df*	MS	F	p
Main Effects	3620.9	8	452.6	64.5	<0.001
Site	408.6	1	408.6	58.2	<0.0001
Size	1530.1	4	382.5	54.5	<0.001
Season	1263.9	3	421.3	60.0	<0.001
2–Way Interactions	865.5	19	45.5	6.5	<0.001
Site x Size	46.2	4	11.5	1.6	0.16
Site x Season	304.2	3	101.4	14.4	<0.0001
Size x Season	504.4	12	42.0	5.9	<0.0001
Site x Size x Season	169.57	12	14.1	2.0	0.02
Explained	4641.1	39	119.0	16.9	<0.0001
Residual	7018.9	1000	7.0		
Total	11660.3	1039	11.2		

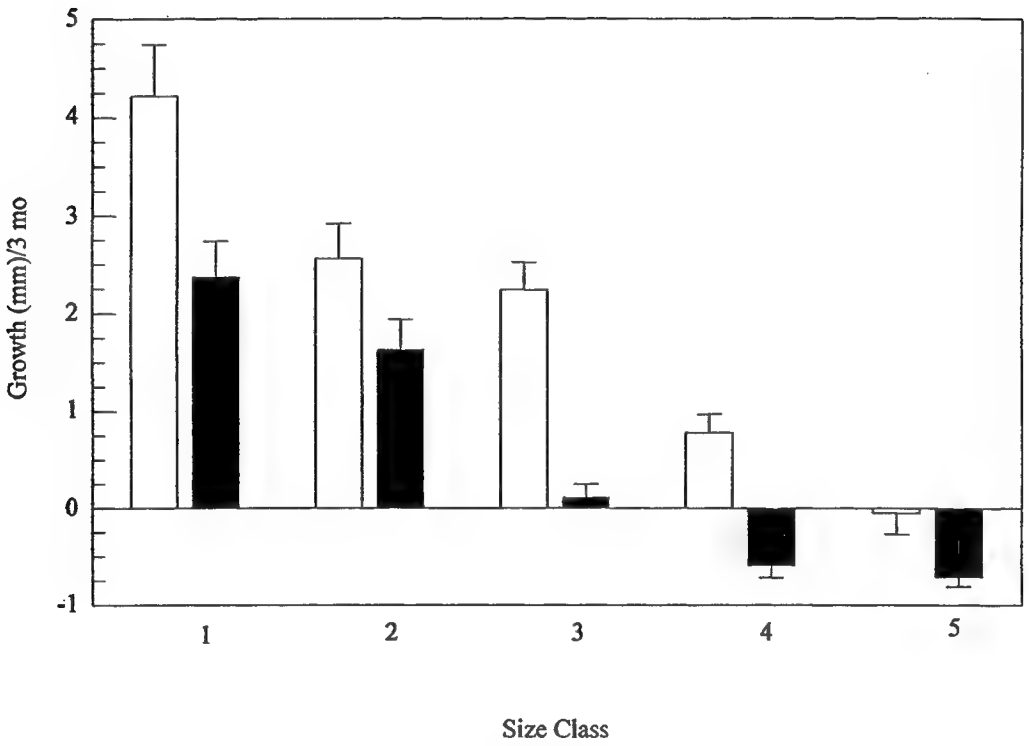

Figure 4.3: Mean growth rates of clams in size classes 1–5 for "clean" (open bars) and "contaminated" (filled bars) sites. Means are over individuals and seasons. Negative growth rates are due to normal wear and chipping of shells of larger clams, which do not grow as rapidly as their shells are worn down. Error bars represent one standard error.

showing that they each explain significant amounts of the difference in fates. The interaction of time and location (FTL, SFTL) was also highly significant. The mean (over sites and times) of survival frequencies was higher at the "contaminated" site (0.83) than at the "clean" site (0.54), and most of this difference occurred in the summer and fall (Figure 4.4).

For a general picture of differences in growth and survival between all the sites, we compared multiway contingency tables of initial state and subsequent fate of clams by general log-linear model fitting. This analysis was identical to that for survival, except that fates were not dead/alive, but were: size classes 1'–5', dead, or missing. Contingency table analysis results (Table 4.6) show highly significant season and site effects, even when both factors are included in the model. This is evidence that seasonal matrices calculated from these contingency tables are significantly different from one another.

Sites were also compared with log–linear analysis seperately by season to try to break down the effects of the full multiway tables. This simpler analysis tested the saturated (SFL) against the SL, SF model to find the significance of the FL, SFL model. There were highly significant differences between sites in all seasons but winter (Table 4.7).

Growth rates across the entire size spectrum at each site, for each season, were compared in Walford plots of length at time t against length at time $t + 1$ (Walford, 1946). Sites were compared for difference in slope of linear regressions through Walford plots by analysis of covariance of length data (McCuaig and Green, 1983). Tests for the homogeneity of slope for regression lines of Walford plots for each season (Figure 4.5) were significant in all seasons, indicating that the slopes did differ (Table 4.8). However, in fall and winter (but not spring or summer), if Barnstable Harbor is removed from the analysis, the other sites do not differ significantly from one another, suggesting that the slope of the Barnstable Harbor line is different enough from the others to cause the non-significant result.

Table 4.5: Results of Log–Linear Analysis of Effects of Site (L), Season (T), and Size Class (S) on Fate (F). Fates are being dead or alive. The two models that were compared to calculate G^2 and degrees of freedom for each set of factors being tested are shown above the horizontal lines.

Model	G_2	df	P
STL, SF	512.5	35	
STL, SFT	151.8	20	
FT, SFT	360.7	15	<0.0001
STL, SF	512.5	35	
STL, SFL	384.9	30	
FL, SFL	127.6	5	<0.0001
STL, SFT	151.8	20	
STL, SFT, SFL	36.5	15	
SFT, FT	115.3	5	<0.0001
STL, SFL	384.9	30	
STL, SFL, SFT	36.5	15	
SFT, FT	348.4	15	<0.0001
STL, SFL, SFT	36.5	15	
SFTL	0	0	
FTL, SFTL	36.5	15	0.001

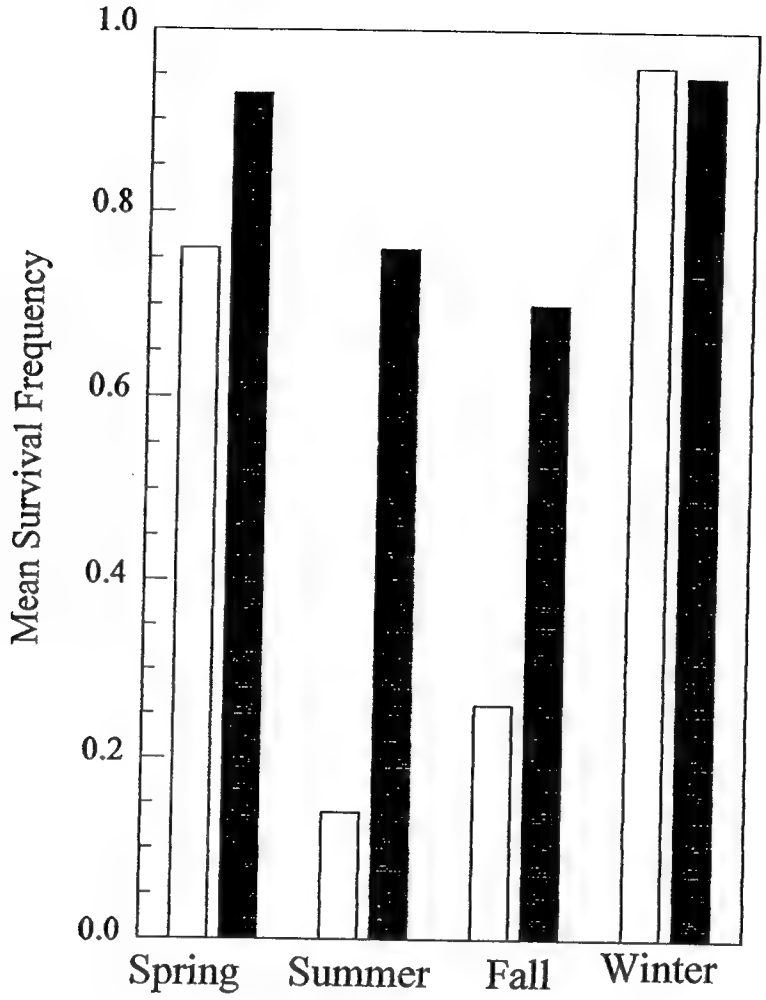

Figure 4.4: Survival frequencies by season. Means are over individuals in all size classes. Open bars are for the "clean" site and filled bars are the "contaminated" site, for each season.

Table 4.6: Results of Log–Linear Analysis of Effects of Site (L), Season (T), and Size Class (S) on Fate (F). Fates are the five size classes, dead, or missing. The two models that were compared to calculate G^2 and degrees of freedom for each set of factors being tested are shown above the horizontal lines.

Model	G_2	df	P
STL, SF	1342.9	570	
STL, SFT	842.1	480	
FT, SFT	500.8	90	<0.0001
STL, SF	1342.9	570	
STL, SFL	917.5	450	
FL, SFL	425.4	120	<0.001
STL, SFT	842.1	480	
STL, SFT, SFL	373.0	360	
FL, SFL	469.1	120	<0.0001
STL, SFL	917.5	450	
STL, SFL, SFT	373.0	360	
FT, SFT	544.5	90	<0.0001
STL, SFL, SFT	373.0	360	
SFTL	0	0	
FTL, SFTL	373.0	360	0.31

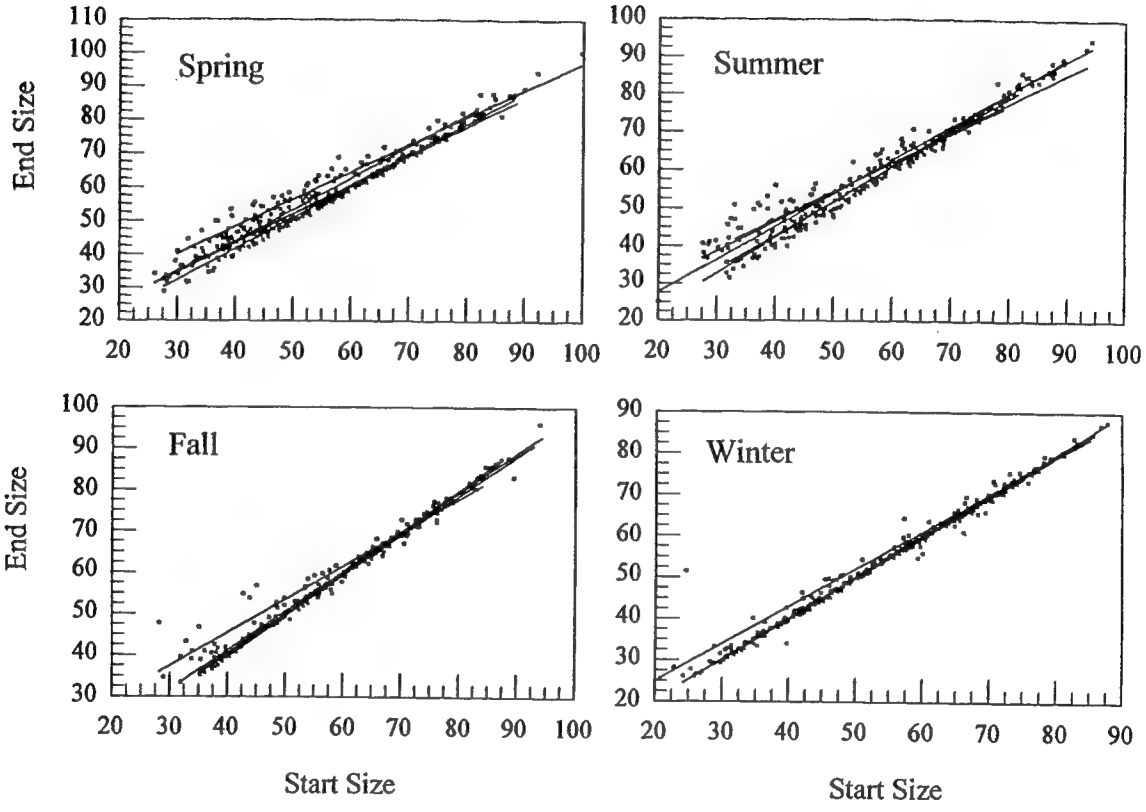

Figure 4.5: Walford Plots of Clam Growth by Season. Length (in mm) at deployment (Start Size) is plotted against length at recovery three months later (End Size) for all clams recovered alive in each season. Lines are regressions of the form $y = a * x + b$ for clams at each site. Regression parameters and comparisons between slopes are reported in Table 4.3.1.

Table 4.7: Log–linear analysis of contingency tables of fate (F) by state (S) in each season. Fates are the five size classes, dead, or missing. For each season, the SL, SF model was compared to the saturated model to test for location effects. The table shows log–liklihood ratios, degrees of freedom, and significance for the FL, SFL model.

Season	G^2	*df*	P
Spring	211.6	120	<0.001
Summer	331.7	120	<0.001
Fall	204.3	120	<0.001
Winter	94.5	120	0.96

Interpretation of these results is complicated by the possibility of having large enough samples (40–80 clams in each regression) that no difference is detectected when in fact there is one (McCuaig and Green, 1983). Walford plots are normally made from measurements of annual bands on bivalve shells, whereas here, we used sequential measurements over three–month intervals. The time interval should not matter, but on our plots, each point is an independent measurement on an individual clam, rather than several points being from the same clam. These results suggest that at least in the fall and winter, small clams in Barnstable Harbor are growing faster in proportion to large clams than are small clams at the other sites.

4.3.2 Reproductive Cycle and Fecundity

Reproductive cycles of clam populations differed between contaminated and uncontaminated sites (Figure 4.6). Both female and male clams from Barnstable Harbor

Table 4.8: Walford Plot Regression Parameters for each site in each season, and the significance of the test for homogeneity of slope. Parameters are the slope, a, and intercept, b, from regressions of the form $y = a * x + b$. Significance values in parentheses are for tests where Barnstable Harbor was removed from analysis.

Season	Site	Slope	Intercept	r^2	Significance
Spring	Barnstable H.	0.81	15.87	0.96	p<0.001
	Fort Point C.	0.85	9.39	0.97	
	Neponset R.	0.93	4.61	0.98	
	Saugus R.	0.86	8.76	0.98	
	Wellfleet H.	0.94	6.22	0.94	
Summer	Barnstable H.	0.88	10.12	0.94	p<0.001
	Fort Point C.	0.74	17.21	0.92	
	Neponset R.	0.77	15.42	0.95	
	Saugus R.	0.90	6.72	0.98	
	Wellfleet H.	0.94	4.33	0.97	
Fall	Barnstable H.	0.81	13.23	0.92	p<0.001
	Fort Point C.	0.99	-0.30	0.99	(p=0.49)
	Neponset R.	0.96	2.00	0.99	
	Saugus R.	0.95	2.22	0.99	
	Wellfleet H.	0.97	2.33	0.99	
Winter	Barnstable H.	0.90	0.93	0.96	p<0.001
	Fort Point C.	0.98	0.87	0.99	(p=0.79)
	Neponset R.	0.98	0.64	0.99	
	Saugus R.	0.98	0.60	0.99	
	Wellfleet H.	0.98	0.50	0.99	

and Wellfleet showed evidence of advanced stages of gamete development and spawning during the late spring through early fall. Populations from the Boston area (Fort Point Channel, Saugus and Neponset River) did not show evidence of spawning until mid-summer and spawning occurred for only a short period of time.

Only 51 ripe females from all sites and times were collected in this sampling program. Because data points were missing for one or more size classes at each site, size–specific fecundities (M_i) could not be calculated for each site. Pooled data from all sites and seasons was used to estimate M_i for each size class 1–5 as 0.03, 0.08, 0.12, 0.27, and 0.52. Fecundities were not normally distributed, so egg numbers were log–transformed to produce normal distributions before analysis. Differences in fecundity between "clean" and "contaminated" sites by size class and sampling month were tested by 3–way ANOVA. Sampling month was not significant (p=0.22), and cases were missing, so it was removed as a factor, and site was tested by size class in a 2–way ANOVA (Table 4.9). No difference was detected between eggs per female of "clean" ($\overline{X} = 15.98 \pm 0.19$, n=31) and "contaminated" ($\overline{X} = 15.71 \pm 0.19$, n=14) sites (p=0.37). The site by size interaction was not significant (p=0.63).

4.3.3 Recruitment and Population Structure

Populations of clams at the five sites showed differing patterns of size-class frequencies and population density in 1995 and 1996 (Figure 4.7). The Neponset River site had the highest density in both years. Recriutment by year at "clean" and "contaminated" sites was tested by 2–way ANOVA. Recruits (clams< 40 mm) per area did not differ significantly at the 0.05 level between "clean" ($\overline{X} = 1.8 \pm .57$) and "contaminated" ($\overline{X} = 0.95 \pm 0.15$) sites(Table 4.10). Recruits per area did differ between years (p=0.01), and the interaction between site and year was also significant (p<0.001). Recruitment by year was also tested by 2–way ANOVA as recruits per adult, since this was calculated for model parameter estimates. Recruits per adult (r in the model) differed significantly between "clean" ($\overline{X} = 0.46 \pm 0.18$) and "contaminated"

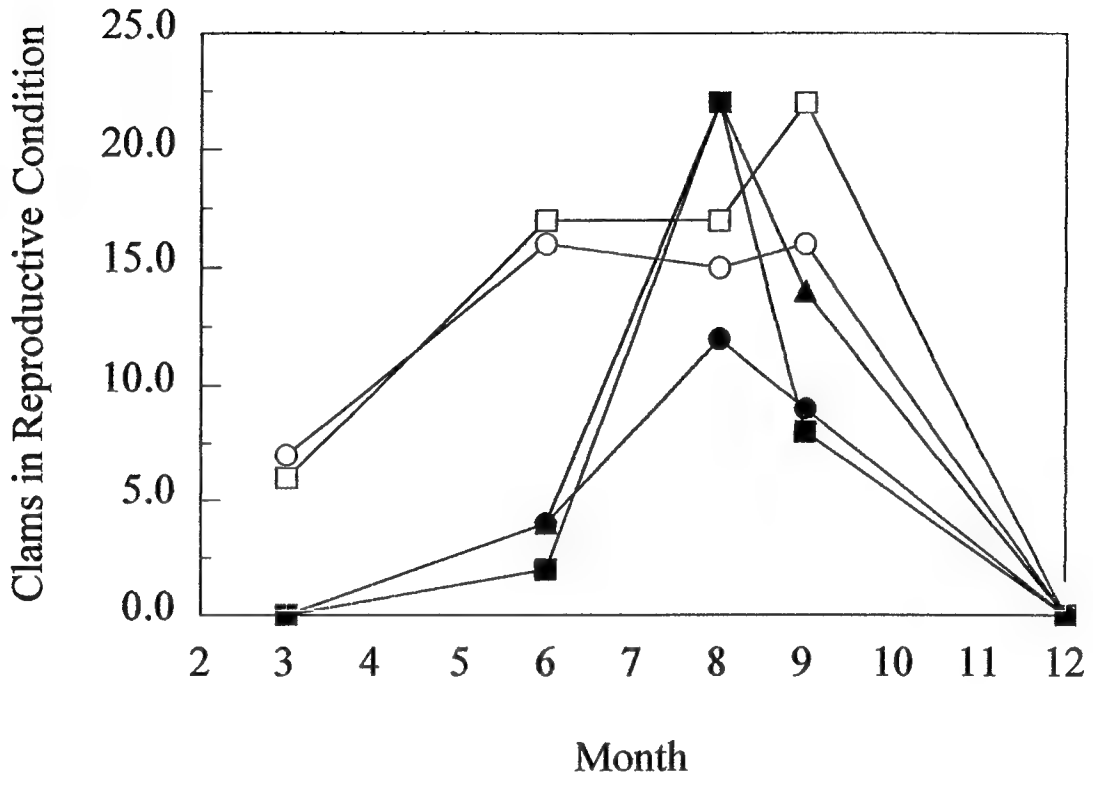

Figure 4.6: Reproductive Cycle of *Mya arenaria* at each site over a one–year period. Months of the year are labelled from 1 (January) to 12 (December). Number of clams out of samples (n=25) collected in March, June, August, September, and December 1995 in a reproductive condition (late developing, ripe, or spawning) are shown for each site. Open symbols are uncontaminated sites and filled symbols are contaminated sites. Sites are Barnstable Harbor (open circles), Fort Point Channel (filled triangles), Neponset River (filled circles), Saugus River (filled squares), and Wellfleet Harbor (open squares).

Table 4.9: ANOVA table for fecundity.Source of variation (Source) is explained by the sum of squares (SS), degrees of freedom (*df*), mean square (MS), F statistic (F), and significance (p).

Source of Variation	SS	*df*	MS	F	Sig. of F
Main Effects	17.2	5	3.4	10.2	<0.001
Site	0.3	1	0.3	0.8	0.37
Size	17.1	4	4.3	12.8	<0.001
Site x Size	0.8	4	0.2	0.6	0.63
Explained	27.4	9	3.0	9.1	<0.001
Residual	11.7	35	0.3		
Total	39.1	44	0.9		

($\overline{X} = 0.15 \pm 0.03$) sites at the 0.001 level (Table 4.10). Year and the site-by-year interaction were also significant ($p<0.001$). There are fewer degrees of freedom for this test because recruits per adult could not be calculated in samples where there were no adults. Values for recruits per adult depend on the density of adult populations, and since adult densities are higher at contaminated sites but raw recruitment does not differ, recruitment per adult is higher at clean sites.

4.3.4 Model Analysis Results

According to results of the histological examination of gonad samples, clams in Barnstable and Wellfleet Harbors spawned throughout the spring and summer, whereas clams from the Boston area sites reproduced during a short period of time in late summer. This pattern was approximated in the model by having reproduction occur during spring and summer for Barnstable and Wellfleet, and only during the summer at the Boston sites. At these times, the elements of the first row of the seasonal matrix were calculated by Equation 4.2, using measured values of M_i (Section 4.3.2) and r (Table 4.18). $R_i = 0$ in seasons when reproduction is not occurring. Only the lower right portion (Table 4.2) of seasonal matrices containing P_i and G_{ij} for i, j =1–5 are reported (Table 4.11, Table 4.12, Table 4.13, Table 4.14, and Table 4.15), since G_{ij} for stages A, B, and C are always one.

At each site, elasticities to each parameter were consistent across the seasons. The largest element of each matrix (Table 4.16) contributed from 74–100% to λ. All of these parameters were stasis parameters (P_i), for the largest size class at clean sites, and for the second or third size class at the other sites.

The annual projection matrices (Table 4.3.4) summarize the differences among the sites more clearly than do the seasonal matrices. Parameters in these matrices are calculated from all the ways clams can make each transitions during a year. Matrices with more entries below the diagonal reflect faster growth between size classes, and the sums of columns reflect survival rates by size class. Clam populations at Wellfleet

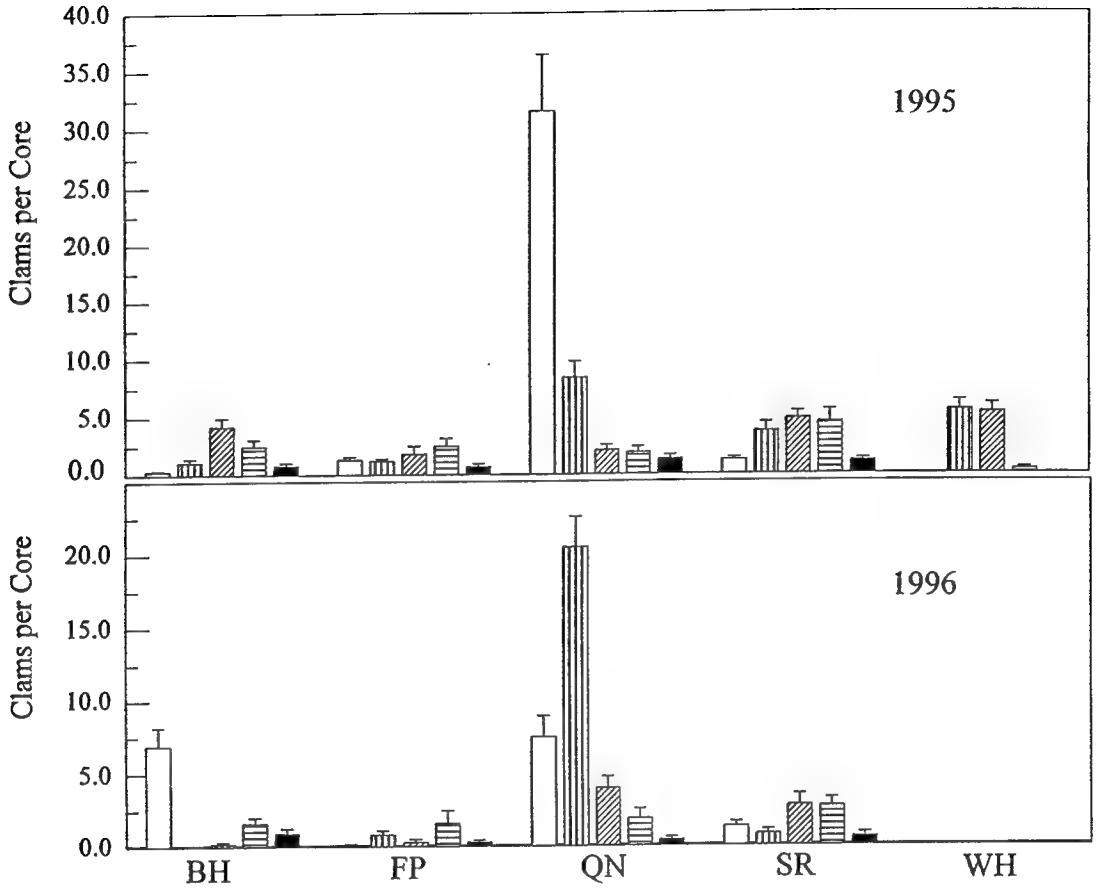

Figure 4.7: Clam Population Structures in 1995 (upper panel) and 1996 (lower panel). For each site on the x-axis—BH (Barnstable Harbor), FP (Fort Point Channel), QN (Neponset River), SR (Saugus River), and WH (Wellfleet Harbor)—the five bars show the mean number of clams in ten 30 cm diameter cores for each size class: 1 (open bars); 2 (vertical lines); 3 (diagonal lines); 4 (horizontal lines), and 5 (filled bars). Error bars represent one standard error over the ten replicate cores.

Table 4.10: ANOVA tables for testing raw recruitment (clams<40 mm/core (30 cm diameter)) and recruits per adult.

Source of Variation	SS	*df*	MS	F	Sig. of F
Raw Recruitment					
Main Effects	51.4	2	25.7	4.6	0.013
Year	37.8	1	37.8	6.8	0.011
Site	13.6	1	13.6	2.4	0.122
Year x Site	74.1	1	74.1	13.3	<0.001
Explained	125.5	3	41.8	7.5	<0.001
Residual	423.4	76	5.6		
Total	548.9	79	6.9		
Recruits per Adult					
Main Effects	11.9	2	5.9	33.9	<0.001
Year	8.2	1	8.2	46.4	<0.001
Site	6.7	1	6.7	37.9	<0.001
Year x Site	9.6	1	9.6	54.5	<0.001
Explained	15.8	3	5.2	29.9	<0.001
Residual	10.2	58	0.18		
Total	26.1	61	0.4		

Table 4.11: Barnstable Harbor seasonal projection matrices

Winter	0.71	0	0	0	0
	0.286	0.92	0	0	0
	0	0	0.818	0	0
	0	0	0.182	1	0
	0	0	0	0	0.933
Spring	0	0	0	0	0
	1	0.333	0	0	0
	0	0.407	0.143	0	0
	0	0.074	0.429	0.25	0
	0	0	0.429	0.25	0.867
Summer	0	0	0	0	0
	0.1	0.143	0	0	0
	0	0.0476	0	0	0
	0	0.0476	0.1	0	0
	0	0	0.1	0	0.333
Fall	0.111	0	0	0	0
	0.333	0.286	0	0	0
	0	0.0952	0.4	0	0
	0	0	0	0	0
	0	0	0	0	0.333

Table 4.12: Fort Point Channel seasonal projection matrices. Arbitrary parameters added to make annual matrix reducible are in bold.

Winter	1	0	0	0	0
	0	1	0	0	0
	0	0	1	0	0
	0	0	0	0.75	0
	0	0	0	0	0.8
Spring	0.667	0	0	0	0
	0.333	0.733	0	0	0
	0	0.133	1	0	0
	0	0	0	1	0
	0	0	0	0	0.786
Summer	0.5	0	0	0	0
	0.25	1	0	0	0
	0	0	0.5	0	0
	0	0	0.5	0.6	0
	0	0	0	0	0.5
Fall	0	0	0	0	0
	0.01	1	0	0	0
	0	0	**0.01**	0	0
	0	0	**0.01**	**0.01**	0
	0	0	0	**0.01**	0.0526

Table 4.13: Neponset River seasonal projection matrices. Arbitrary parameters added to make annual matrix reducible are in bold.

Winter	0.833	0	0	0	0
	0.0833	0.944	0	0	0
	0	0	1	0	0
	0	0	0	0.75	0
	0	0	0	0.75	0
	0	0	0	0.25	0.733
Spring	0.917	0	0	0	0
	0.083	0.958	0	0	0
	0	0	0.727	0	0
	0	0	0	1	0
	0	0	0	0	0.556
Summer	0.222	0	0	0	0
	0.778	0.773	0	0	0
	0	0.091	0.75	0	0
	0	0	**0.01**	0.5	0
	0	0	0	0	0.682
Fall	0.667	0	0	0	0
	0.25	1	0	0	0
	0	0	1	0	0
	0	0	0	1	0
	0	0	0	0	0.636

Table 4.14: Saugus River seasonal projection matrices. Arbitrary parameters added to make annual matrix reducible are in bold. Parameters for winter matrix were estimated from data collected in 1996. All other data was collected in 1995.

Winter	1	0	0	0	0
	0	1	0	0	0
	0	0	1	0	0
	0	0	0	0.83	0
	0	0	0	0.083	0.96
Spring	0.688	0	0	0	0
	0.313	0.885	0	0	0
	0	0.0769	1	0	0
	0	0	0	1	0
	0	0	0	0	0.93
Summer	0.167	0	0	0	0
	0.667	0.937	0	0	0
	0	0.0625	1	0	0
	0	0	**0.01**	0.75	0
	0	0	0	0.25	0.619
Fall	0.833	0	0	0	0
	0.167	1	0	0	0
	0	0	1	0	0
	0	0	0	1	0
	0	0	0	0	0.958

Table 4.15: Wellfleet Harbor seasonal projection matrices. Arbitrary parameters added to make annual matrix reducible are in bold.

Winter	1	0	0	0	0
	0	0.963	0	0	0
	0	0	0.917	0	0
	0	0	0.083	0.889	0
	0	0	0	0	0.972
Spring	0.077	0	0	0	0
	0.308	0.259	0	0	0
	0	0.185	0.5	0	0
	0	0.074	0.5	0.6	0
	0	0	0	0.4	0.75
Summer	0	0	0	0	0
	0.01	0	0	0	0
	0	0.034	0	0	0
	0	0	0.2	0	0
	0	0	0	0.083	0.087
Fall	0	0	0	0	0
	0.091	0.055	0	0	0
	0	0	0.4	0	0
	0	0	0.2	0.2	0
	0	0	0	0	0.217

Table 4.16: Seasonal Elasticities. Only the largest element of elasticity matrices for each season and site are reported since the other elements are negligible in comparison. Barnstable Harbor(BH), Fort Point Channel(FP), Neponset River (QN), Saugus River (SR), and Wellfleet Harbor (WH).

	Site				
	BH	FP	QN	SR	WH
Element	P_5	P_2	P_2	P_3	P_5
Spring	0.89	0.99	0.75	0.97	1
Summer	0.90	0.99	0.83	0.97	1
Fall	0.91	0.99	0.74	0.97	1
Winter	0.91	0.99	0.75	0.97	1

are clearly limited by survival, while growth rates are highest at Barnstable Harbor. Survival rates are highest at Neponset River and Saugus. When λ is calculated from the annual matrices, Barnstable and Wellfleet Harbors have the lowest population growth rates (Table 4.3.4). The highest elasticities in seasonal matrices were to stasis parameters, P_i, which suggests that survival may be important for *M. arnearia* populations. The relative magnitude of λ is robust to changes in r over several orders of magnitude, and in fact does not change population growth rate by more than 0.01 even when varied over a wide range (Table 4.3.4), as is expected given the low elasticity to these parameters. Population growth is higher at contaminated sites than at uncontaminated ones (Figure 4.8).

Population growth rate for the "clean" site matrix was 0.046, and for the "contaminated" site matrix it was 0.79, which are close to the means of the population growth rates of the matrices used to calculate the "clean" (Barnstable and Wellfleet) and "contaminated" (Fort Point and Saugus) site matrices. The largest elements of the seasonal LTRE decomposition matrices, $\mathbf{D}_s$, (Table 4.19) are those which are principally responsible for the observed difference in population growth rates between the two populations. By far the largest element in each seasonal matrix is stasis in size class 2 (40–55 mm clams), indicating that the difference in λ is mostly due to differences in this parameter. This result is in agreement with the results of the elasticity analysis, although they do not necessarily always agree. In the seasonal matrices, P_2 at clean sites were less than 0.3 (except in winter when P_2 was 0.9) while it was greater than 0.7 in all seasons at contaminated sites. The importance of this element is highest in summer and fall. Positive elements of $\mathbf{D}_s$ are ones which were larger in $\mathbf{A}^{FS}$, and negative ones were larger in $\mathbf{A}^{BW}$. Although elements of $\mathbf{A}^{BW}$ are larger for reproduction and growth through the size classes, changes in these elements do not contribute as much to changes in λ as do the elements for stasis, which are higher in $\mathbf{A}^{FS}$.

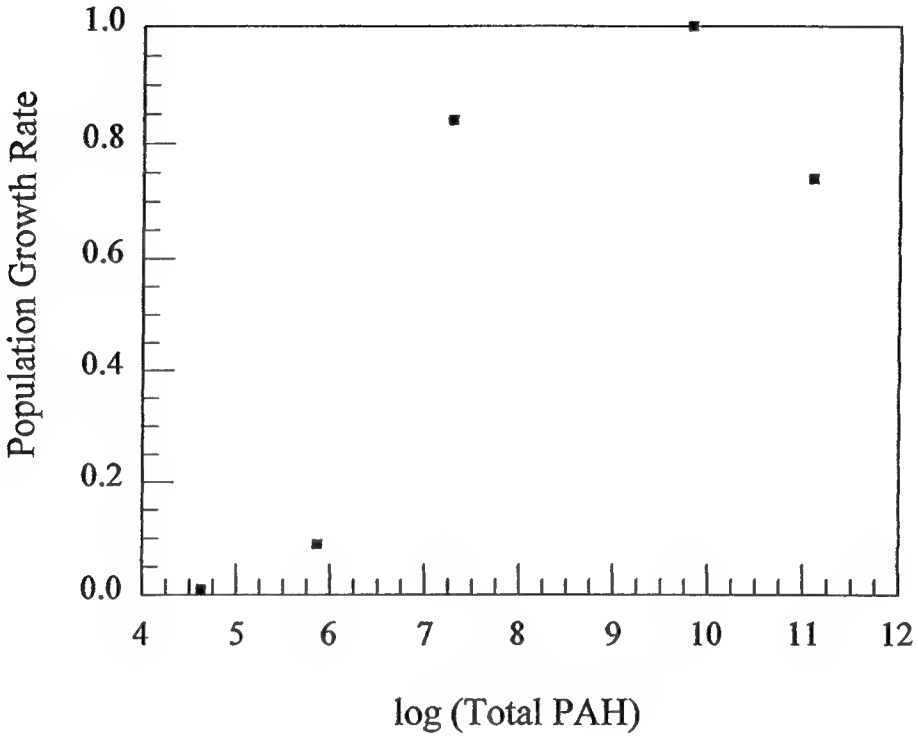

Figure 4.8: Population Growth Rate vs. PAH Concentration. Population growth rates for each site are plotted against the logarithm of total PAH concentration (in ng/g dry weight) at the site. Sites are, from left to right, Wellfleet Harbor, Barnstable Harbor, Neponset River, Saugus River, and Fort Point Channel.

Table 4.17: Annual Matrices. Measured recruitment from 1995 was used to calculate R_i, then the four seasonal matrices were multiplied together for each site. Parameters in these matrices include all possible ways clams could make each transition during one year. Elements below the first subdiagonal represent growth through more than one stage, which is not possible in one season, but common over one year.

Barnstable Harbor	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
	0	0	0.001	0.002	0.002	0.007	0.004	0.009
	0.710	0.079	0	0.001	0.002	0.002	0.005	0.010
	0.286	0.338	0.026	0.038	0.012	0	0	0
	0	0	0.008	0.027	0.009	0	0	0
	0	0	0.002	0.006	0.002	0	0	0
	0	0	0	0	0.013	0.049	0.026	0.090
Fort Point Channel	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
	0	0	0.003	0.005	0.008	0.013	0.028	0.0430
	1.000	0	0	0	0	0	0	0
	0	0.010	0.255	0.503	0.733	0	0	0
	0	0	0	0	0.001	0.005	0	0
	0	0	0	0	0.001	0.008	0.004	0
	0	0	0	0	0.001	0.004	0.005	0.0165
Neponset River	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
	0	0	0.034	0.039	0.088	0.100	0.311	0.333
	0.833	0.556	0.123	0.113	0	0	0	0
	0.083	0.292	0.799	0.793	0.699	0	0	0
	0	0	0	0.008	0.087	0.545	0	0
	0	0	0	0	0	0.005	0.375	0
	0	0	0	0	0	0.002	0.125	0.177
Saugus River	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
	0	0	0.001	0.002	0.004	0.005	0.012	0.022
	1.000	0.833	0.139	0.096	0	0	0	0
	0	0.167	0.695	0.771	0.829	0	0	0
	0	0	0	0.020	0.132	1.000	0	0
	0	0	0	0	0.001	0.008	0.622	0
	0	0	0	0	< 0.001	0.001	0.292	0.530
Wellfleet Harbor	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
	1.000	0	0	0	0	0	0	0
	0	0.088	0.001	< 0.001	0	0	0	0
	0	0	0	0.004	0.003	0	0	0
	0	0	0	0.002	0.008	0.018	0	0
	0	0	0	0	0.001	0.009	0.018	0.014

Table 4.18: Population Growth Rates. Recruits per adult, r, and population growth rates, λ, calculated using measured recruitment rates for each site, the minimum measured recruitment rate, $r = 0$, and the maximum measured recruitment rate, $r = 2.3$.

Site	r	λ_r	λ_{min}	λ_{max}
Barnstable H.	0.04	0.09	0.09	0.21
Wellfleet H.	0	0.01	0.01	0.07
Saugus R.	0.09	1.00	1.00	1.08
Neponset R.	2.3	0.84	0.70	0.84
Fort Point C.	0.21	0.74	0.73	0.76

4.4 Discussion

Numerous studies on marine bivalves have shown negative effects of contaminant exposure on individual physiological processes. Populations of *Mya arenaria* living at contaminated sites are predicted to be composed of unhealthy individuals. In fact, McDowell and Shea (1996) report that physiological condition of *M. arenaria*, as measured by digestive gland-gonad condition index, dry weight of the digestive gland-gonad complex, and the lipid weight of the digestive gland-gonad complex, was significantly lower at the contaminated sites used in this study than at the clean sites. These results are similar to those reported by Capuzzo *et al.* (1989) for transplanted mussels (*Mytilus edulis*) in New Bedford Harbor, where reduced condition indices and lipid accumulation correlated with reduced reproductive effort. Clams at the contaminated sites were not only energetically inferior to clams at clean sites, but also had significantly higher incidence of the disease hematopoietic neoplasia, and of

Table 4.19: Life Table Response Experiment Decomposition Matrices. Elements in decomposition matrices correspond to seasonal matrix elements. The sum of the elements of all these matrices is approximately equal to the difference between the population growth rates of the "clean" and "contaminated" sites. Negative values are parameters that were larger in the "clean" matrices; positive values are parameters that were larger in the "contaminated" matrices.

Spring	0	0	0	< 0.001	-0.001	-0.001	-0.001	-0.002
	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
	0	0	0	0.003	0	0	0	0
	0	0	0	-0.002	0.095	0	0	0
	0	0	0	0	-0.01	0.02	0	0
	0	0	0	0	-0.002	-0.006	0.007	0
	0	0	0	0	0	-0.005	-0.006	0.001
Summer	0	0	0	< 0.001	0.002	0.003	0.006	0.013
	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
	0	0	0	0.012	0	0	0	0
	0	0	0	0.019	0.176	0	0	0
	0	0	0	0	-0.001	0.047	0	0
	0	0	0	0	-0.001	0.002	0.013	0
	0	0	0	0	0	-0.002	0.003	0.013
Fall	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
	0	0	0	0.006	0	0	0	0
	0	0	0	-0.002	0.159	0	0	0
	0	0	0	0	-0.004	0.006	0	0
	0	0	0	0	0	-0.003	0.014	0
	0	0	0	0	0	0	< 0.001	0.011
Winter	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
	0	0	0	0.001	0	0	0	0
	0	0	0	-0.001	0.007	0	0	0
	0	0	0	0	0	0.004	0	0
	0	0	0	0	0	-0.002	-0.002	0
	0	0	0	0	0	0	0.001	-0.002

cell proliferation, an abnormality in gonadal tissue. Despite the significance of these physiological impairments, we found that population growth rates were highest at the contaminated sites.

Higher population growth rates at contaminated sites are suggested by the higher densities of clams present at these sites. However, the reason that these populations are dense was unknown, and could not be predicted by information on individual physiological processes alone. By integrating clam survival, growth and reproduction in matrix population models, we found that survival of clams plays the largest role in determining population growth rates. This was confirmed by elasticity analysis and LTRE decomposition. Clams at contaminated sites had higher survial rates than clams at clean sites. Although shell growth rates were higher at clean sites, survival plays a larger role in population growth rate, leading to faster-growing populations at the contaminated sites. Fecundities and recruitment did not differ between contaminated and clean sites, but even if they had, the impact on population growth rate would be small because of small elasticities to the reproductive parameters in the model. Although many studies have shown laboratory effects of contaminants on reproduction, larval survival, and energy budgets on marine bivalves, the strength of these effects on *M. arenaria* and their importance in the field were insufficient to cause low population growth rates.

Sub–lethal changes in clam physiology cannot be used to explain differences in survival rates. Factors directly causing death during a three–month time period must be responsible for the differences in survival between these sites. It is possible that different survival rates could be due to different predation rates. Although predators were not carefully monitored in this study, we could count mortality due to moon snails (*Lunatia heros*) because moon snails leave a characteristic drill hole in the shells of clams that they have eaten. For example, 25% of summer mortality was due to moon snail predation at Wellfleet, but evidence of moon snail predation was never observed at the contaminated sites. Clams at Wellfleet Harbor were also

heavily preyed upon by the milky ribbon worm, *Cerebratulus lacteus*, during the spring and summer (pers. obs. and pers. com., Paul Sommerville, Wellfleet Shellfish Biologist). This worm appears sporadically in high abundance on clam flats and has been know to eliminate clam populations with low recruitment rates (Rowell and Woo, 1990). Although *C. lacteus* is a characteristic member of the fauna found in contaminated sites in the New York Bight (Chang *et. al.*, 1992), it was not observed at the contaminated sites in this study. It is possible that predators are more sensitive to contaminants than are clams. The hypothesis that high population growth rates of clams at Neponset River and Saugus River are due to lower abundance of predators deserves further investigation.

The comparison between the λ_r and λ_{min} and λ_{max} shows that the value used for recruitment in the model can be changed over three orders of magnitude and the population growth rate is changed very little. Errors in estimation of recruitment of several orders of magnitude would therefore not change the observed trends in population growth rates. This is backed up by the elasticity analysis. Several assumptions had to be made to estimate recruitment, but since recruitment has so little impact on population growth rates, the validity of these assumptions is not very important to the results of the model. The fact that Barnstable and Wellfleet clams are reproducing in two seasons rather than one apparently had little importance, since these sites still have dramatically lower population growth rates than the Boston sites. The difference in spawning times is worthy of note, however because populations of *M. arenaria* in Maine are not even spawning as late as the Boston area sites (pers. comm., B. Beale). Spawning is triggered by water temperatures, so clams in Massachusetts should be spawning before clams in Maine, where waters are colder.

The results reported here indicate that populations may be decreasing quite rapidly at most of the sites, and only growing at Saugus. Population surveys made in June 1996 (Figure 4.7), showed that the projections of the 1995 model were not unreasonable. A rapid decline in the Wellfleet population was expected, and in fact,

no clams were found in the study area in June 1996. The Barnstable population was also projected to decrease rapidly. In June 1996, the total population density had increased to 9.6 $\pm$ 3.41 clams per core. This was due to a large, successful recruitment event, since 70% of the clams were obviously less than a year old (mostly <30 mm). Only about 30% of the clams in 1996 were in size classes 3, 4, and 5. This roughly translates to a population density decrease to 60% of that of the previous year, if recruitment is ignored, which is a large decrease, as predicted by the model.

The low population growth rates reported here are also not totally accurate, since Ripley and Caswell (in prep.) have shown that using highly variable stochastic recruitment in a matrix model instead of a single value for recruitment allows populations to grow at a faster rate, and is a more realistic representation of population processes. This technique was not used here because it requires data on the range of intensity in recruitment events over many years, which were unavailable for these sites. However, recruitment was shown to vary from year to year in this study. The comparison between sites would probably have the same result using the stochastic method unless extent of variability in recruitment differs substantially between sites.

Populations of bivalve molluscs chronically exposed to contaminated habitats may be highly resistant to contaminant effects (McDowell Capuzzo, 1996). In this study, we found that population growth of *Mya arenaria* was enhanced by contamination. It is possible that genetic differences between populations at these sites contribute to the observed contaminant tolerances. Circulation studies (Geyer *et al.*, 1992) of the Massachusetts Bay system suggest that retention time in the Bay is on the order of three weeks—longer than the two–three week larval period of *M. arenaria.* This suggests that larvae released in Cape Cod Bay are probably retained there until they settle. Boston area populations are probably subsidized by larvae from populations farther north. Their larvae are probably swept southward by the consistent counterclockwise circulation pattern in Massachusetts Bay (Geyer *et al.*, 1992). All populations probably do not come from one well-mixed larval pool, although Boston

sites and Cape Cod sites may see separate, mixed pools. These conclusions are based on the assumption that larvae released over tidal mudflats become entrained into the general circulation pattern of deeper water.

The supply of larvae imported to contaminated sites from sites farther north may be sufficient to overcome any potential reproductive impairments. In a larval settlement assay, Wintermeyer *et al.* (1996) showed that *M. arenaria* settled equally well on sediment from all of the sites studied here, except for Wellfleet Harbor. High organic matter (16.8%) and low oxygen levels in the Wellfleet sediments may explain the reduced settlement success at this site. This suggests that although larvae have been shown to be highly susceptible to contaminants in laboratory experiments, they are able to settle and metamorphose when transported to contaminated sites under field conditions.

Although many studies have shown deleterious effects on contaminant exposure on marine bivalves, the kind of sublethal impairments demonstrated by these studies were not observed to lead to reduced population levels at contaminated sites in this study. *Mya arenaria* is a species which is quite tolearant to contaminant stress, so our results may not apply to less hardy species, however it is impossible to study natural populations of those species at contaminated sites in the field. We have shown that it is important to consider other ecological factors, such as predation rates, and life cycle factors, such as potential variation in recruitment, when evaluating contaminant effects on field populations.

4.5 Summary

1. Clams at clean sites grew (in shell length) significantly faster than those at contaminated sites, but clams at contaminated sites had higher survival rates. No differences were found in fecundity or recruitment (by area), although reproductive season was shorter at contaminated sites and recruitment (per adult) did differ.

2. Population growth rates calculated in matrix population models were highest at contaminated sites.

3. Differences between mortality rates (possibly due to predation) and long-term recruitment patterns at the sites may have more of an influence on the dynamics of clam populations than contaminant exposure.

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Chapter 5

Conclusion

The results of this thesis show that the life history traits of a marine bivalve can have important consequences for the effects changes in the environment will have on populations of the bivalve. For the soft shell clam, a broadcast spawner, the highest elasticities are for stasis, that is, survival without growth. According to the literature data on several broadcast spawning species, this was especially true for those species with longer life spans. Life span is important because a broadcast spawning reproductive mode leads to uncertain recruitment success in each year. However, the longer the life span, the more chances the population has to experience a successful recruitment event. In fact, variation in recruitment levels actually increases the population growth rate over that at mean recruitment levels. Analysis of data on vital rates of clams at clean and contaminated sites showed that in fact, survival rates were the most important contributors to differences between the sites studied. Although clams at clean sites grew (in shell length) faster, the populations at contaminated sites were growing faster because of significantly higher survival rates. Lower predation rates at contaminated sites are a possible cause of the different survival rates. Populations of clams at contaminated sites appear to be structured by the combination of long–term recruitment patterns and other ecological factors such as predation, rather than only by contaminant effects on individual clams. A different study animal with different

life history traits, such as a brooding bivalve, might show a more direct response to contaminant exposure if the effects of the toxicant were on a process that contributed strongly to population growth rate.

Appendix A

Untangling Microhabitat Variability in Growth Rates of Soft Shell Clams from Contamination Affects on Growth

A.1 Introduction

Determining the factors responsible for patterns in growth rates of bivalves over large and small spatial scales has been difficult because variability is high and multiple factors contribute to growth rates. Brousseau failed to find any latitudinal gradient in growth rates of the ribbed mussel, *Geukensia demissa* (Brousseau, 1984) or the soft-shell clam, *Mya arenaria* (Brousseau, 1979), concluding that local environmental conditions play a large role in bivalve growth. However, in a more ambitious study of *M. arenaria* growth from Maryland to Nova Scotia, a trend of faster growth at lower latitudes was detected using principle component analysis (Appledoorn, 1983). The two other components explaining variation were sediment siltiness and hydrocarbons, both negatively correlated to growth rates. Growth rate depressions in *G. demissa* in

central Jamaica Bay, New York (near Kennedy airport) have been suggested to be in part due contaminant stress (Franz and Tanacredi, 1993). Hydrocarbon contamination has also been shown to reduce growth rates of clams transplanted to oiled sites, (Dow, 1975; Appledoorn, 1981) suggesting that impaired growth may be an indicator of chronic contaminant exposure.

Untangling any contaminant effect on growth rate from a local site effect requires that other factors known to modify growth rates also be controlled, or at least measured. Early researchers suggested that environmental factors such as food supply (Kellogg, 1905), current speed (Belding, 1930), and sediment qualities (Newcombe, 1935) were responsible for differences in growth rates between sites. Spear and Glude (1956) demonstrated in a reciprocal transplant experiment that environmental qualities of sites, rather than genetic differences between *M. arenaria* sub-populations, were responsible for differing growth rates. That environment, not heredity, controls growth rates has been supported more recently for *Mytilus edulis* (Kautsky *et al.*, 1990), and for *Mercenaria mercenaria* (Landry *et al.*, 1993). A more sophisticated study on *M. mercenaria* (Rawson and Hilbish, 1991) detected heritable variation in juvenile growth rates, but only at the habitats where high and low extremes in growth were measured. Overall, environmental differences accounted for more than 50% of the variation in growth rates in this study.

As an infaunal, intertidal filter feeder, environmental factors likely to affect *Mya arenaria* growth rates include tidal elevation, phytoplankton abundance, flow rates, and sediment composition. Tidal elevation is important because animals living at higher tidal levels will have a shorter period of time each day in which they can filter food, respire, and flush wastes. Newcombe (1935) found that *M. arenaria* in the Bay of Fundy at the eight foot tidal level grew 50% more per year than clams at the sixteen foot tidal level, and that variation in growth was directly correlated with time of submergence. Tidal height is also known to influence growth rates in *G. demissa* (Stiven and Gardner, 1992), and most of the difference is explained by difference

in submergence time (Lin, 1989). A mathematical model for *M. edulis* populations that incorporated food density and time of exposure to air showed that differences in growth rate were due to food availability, not physiological impairments due to exposure (Ross and Nisbet, 1990).

Current flow was cited by Belding (1930) as the most important factor in *M. arenaria* growth. More recent work has explicated this phenomenon. For example, where higher flow rates deliver a higher total amount of food to the clams, faster flows lead to faster growth rates (*Mya*: Emerson, 1990; *Mercenaria*: Grizzle and Morin, 1989). Judge *et al.* (1992) demonstrated by altering rates of flow at contiguous locations at one site that current speed alone does not lead to different growth rates of *M. mercenaria* if chlorophyll *a* concentrations are the same. Thus both current flow and tidal height are important in the amount of food available to the animal at the location, not in-and-of themselves.

Sediment composition has also been shown to affect growth rates in *M. arenaria*. Newcombe (1935) showed that clams in muddy soils with a silty surface layer grew more slowly than in sandier soils. In a sediment and clam reciprocal transplant experiment, Swan (1952) observed that sediment grain size may alter growth rate. In coarser sediments, clams had to grow thicker shells to overcome stronger shell abrasion, and could not grow as fast as a result. Unfortunately this study had very small sample sizes and the results cannot be considered conclusive. Sediment type is a function of flow rates, which are also known to influence growth rates, so decoupling the effect of sediment type from that of flow rate is challenging.

Resuspention of sediment has been reported to have both a positive and a negative effect on growth rates. Under turbid conditions, clams may reduce filtration rate and therefore food intake, reducing growth potential (Grant and Thorpe, 1991). Disturbances that resuspend benthic detritus or diatoms may provide additional food to clams, promoting growth (Emerson, 1990). The relative importance of these effects is yet to be determined.

Food availability has been found to be the strongest correlate to growth rates in many bivalves. A series of papers (summarized in Thompson and Nichols, 1988) on *Macoma balthica*, which co-occurs with *M. arenaria*, have shown that although temperature is strongly correlated with growth rates, it is really phytoplankton production (which is related to temperature) that controls growth rates. Chlorophyll *a* concentrations in the water above clam flats have been found to correlate most strongly to differences in growth rates in *M. mercenaria* (Landry *et al.*, 1993) and *Yoldia notabilis*, a subtidal, infaunal, deposit feeding clam (Nakaoka, 1992).

Several environmental factors have been shown to *not* be important in determining growth rates (when making comparisons within seasons). Newcombe (1935) ruled out temperature, salinity and sulfide concentrations. Temperature and salinity were also found to not have an effect on growth rates in *Yoldia notabilis* (Nakaoka, 1992). Although clam density can affect growth rates, particularly of younger bivalves (*e.g.* Goshima, 1982; Stiven and Gardner, 1992), densities can be controlled in experimental design. It has also been shown in many studies that growth rates decrease with increasing size (*e.g.* Ripley and McDowell, in prep.), but using clams in a limited size range controls this factor.

A synthesis of the importance of these various factors was reported by Grizzle and Morin (1989). In a factorial design field experiment, they tested the interaction of tidal currents, seston, and sediment type. Horizontal seston fluxes were found to be the significant factor. In summary, the potential environmental difference which must be controlled for in order to evaluate growth rates is the amount of food available.

A recent study of populations of *M. arenaria*, around Massachusetts Bay found significantly higher growth rates at uncontaminated sites. (Ripley and McDowell, in prep.). However, in that study growth measurements were made at only one small region of the mud flat at each site, and other factors known to influence growth were not measured. Environmental factors unrelated to contaminant concentrations may have caused the observed growth rates. The study presented here was done to de-

termine whether within-site variation in growth rates was as large as the observed between-site difference in growth rates, when other environmental factors were more carefully controlled. Growth rates over three months in the summer were measured for small *M. arenaria* at five sub-sites in one contaminated and one uncontaminated site. Sediments were analyzed for total organic carbon as a measure of hydrocarbon load, and nitrogen as a measure of phytoplankton detritus (food supply). Mud fraction of sediment was measured, as was immersion time, since these factors may also contribute to growth rates.

A.2 Methods

A.2.1 Sites

Two sites were chosen for this study based on information on sediment contaminant levels (McDowell and Shea, 1997). The contaminated site, the Neponset River in Quincy, MA, has a total sediment PAH concentration of about 1500 ng/g dry weight, while the uncontaminated site, Barnstable Harbor, MA, has a total sediment PAH concentration of about 350 ng/g dry weight. Five locations were selected randomly (with respect to sediment qualities) at each site along the shoreline at approximately equal tidal heights (exposed at mean low water) as sub-sites or plots.

A.2.2 Clam Growth

The smallest clams present in the populations at the two sites were collected in June 1997. Two hundred forty clams from each site were brought to the laboratory overnight and individually numbered in indelible ink and measured. For each site, clams were randomly divided into groups of twelve. Each group was planted in one of four sediment–filled mesh bags at each plot (see Ripley and McDowell, in prep, for more detailed methods). Bags were collected after three months, and clams were

sorted from the sediment by hand and measured.

A.2.3 Immersion Time

Immersion time was measured over one lunar month at each plot. Measurements were made using simple instruments constructed by B. Lancaster at Woods Hole Oceanographic Institution, using Omron electronic hour meters. Meters were sealed into PVC pipes such that coverage by seawater would close the circuit between protruding electrodes and start the meter. Instruments were tested in the laboratory before deployment, and they all counted exactly the same times. Instruments were deployed by burying them into the sediment with just the electrodes sticking up above the sediment surface, and attaching each one to a stake with tie-wraps. Previous measurements of tidal immersion between sites showed less than 10% variation between monthly readings, so only one measurement was made.

A.2.4 Semiment Samples

When plots were set up in June, 1997, duplicate sediment samples were taken at each plot. Sediment from the surface 5 cm was scooped into solvent-rinsed glass jars with a solvent-rinsed aluminum spatula. Sediment was frozen at -10°C immediatley upon return to the lab. Prior to analyses, sediments were refrigerated at 4°C to thaw on November 5, 1997. After thawing, each sample was homogenized by stirring with a solvent-rinsed aluminum spatula. Aliquots of the sample were taken for the following analyses.

Total Organic Carbon and Nitrogen

Approximately 2 g of sediment was dried for 24 hours at 60°C. Dry sediment was ground with a mortar and pestle and approximately 1 g was placed in a plastic urine sample cup. Inorganic carbon was dissolved by adding 20 ml 1 N acetic acid for 24

hours. Up to another 20 ml of acetic acid were added until no more bubbles were observed. Sediments were rinsed three times with distilled water, and filtered onto 0.45 μm millipore paper. Samples were dried for 24 hours at 60°C, weighed, and ground with a mortar and pestle. C:H:N analysis was performed on an Eager 200 automated analyzer.

Sediment Grain Size

Approximately 20 g sediment were placed in tared plastic weigh boats, weighed, and dried for 48 hours at 60°C. The dry sediment was weighed, then rinsed with approximately 250 ml water in a 63μm seive. Sediment remaining in the seive was rinsed onto a pre-weighed glass fiber filter. Sediment on filter (and filter) were replaced into the weigh boat and dried for 48 hours at 60°C. Fraction of sample less than 63μm (the mud fraction) was calculated as 1 – (remaining sediment)/(start weight).

A.3 Results

A.3.1 Clam Growth

In June, the mean length of clams deployed in Barnstable Harbor was 27.9 $\pm$ 0.23 (one standard error), and the mean length of clams in Neponset River was 37.5 $\pm$ 0.17. In September, 46 clams were found alive from Barnstable, and 91 were found alive in Neponset. At least one clam was found at each plot at both sites. At the start of the study clam sizes were different enough between sites that growth rates might be different simply due to starting sizes. Clam growth rates within each site between plots were compared by one–way ANOVA. Although growth differed significantly between plots at each site (Table A.1), there appears to be a difference between growth rates between sites as well (Figure A.1). However, the different starting sizes of clams makes this apparent difference difficult to interpret and test. The slopes of the regressions of growth on start length (Figure A.2) are significantly

Table A.1: ANOVA table for growth between plots for each site. Source of variation (Source) is explained by the sum of squares (SS), degrees of freedom (*df*), mean square (MS), F statistic (F), and significance (p).

Source	SS	*df*	MS	F	p
Barnstable Harbor					
Between plots	341.5	4	85.4	3.08	0.03
Residual	1165	42	27.7		
Total	1506.8	46	32.8		
Neponset River					
Between plots	244.5	4	61.1	9.9	<0.001
Residual	540.1	88	6.1		
Total	784.6	92	8.5		

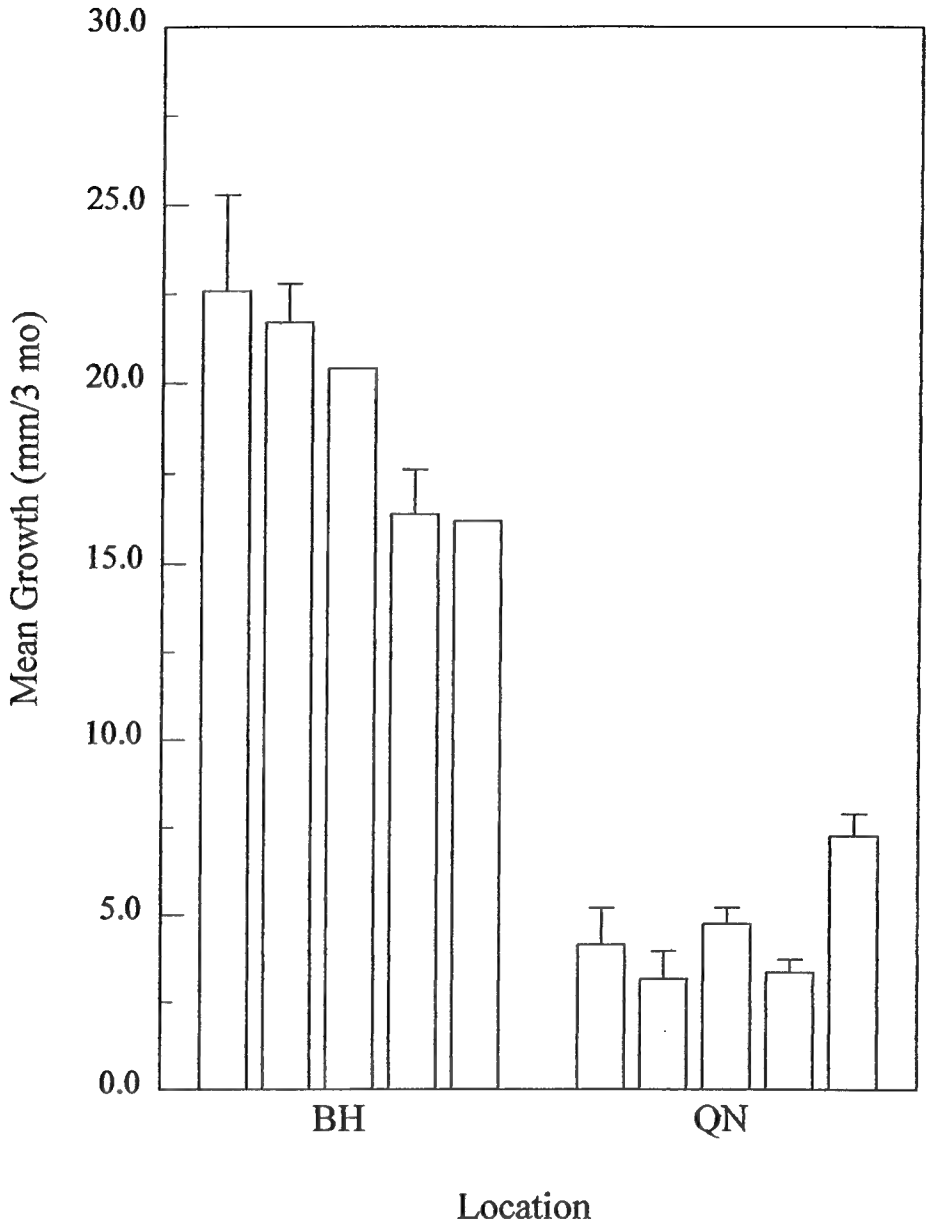

Figure A.1: Clam growth by plot. Mean growth rates (mm/3 mo) over all clams recovered alive in September from each plot (1–5, from left to right) for Barnstable Harbor (BH) and Neponset River (QN). Error bars represent one standard error and where they are not shown the bar represents only one clam.

Table A.2: ANOVA table for slope of regressions of growth on start length between sites. Source of variation (Source) is explained by the sum of squares (SS), degrees of freedom (*df*), mean square (MS), F statistic (F), and significance (p).

Source	SS	*df*	MS	F	p
Within+residual	1666.9	136	12.3		
Site	365.9	1	365.9	29.8	<0.001
Start length	375.7	1	375.7	30.6	<0.001
Site x start length	189.7	1	189.7	15.5	<0.001

different (Table A.2) demonstrating that clams differ in their size–dependent growth rates depending on their location, so an anlysis of covariance cannot be done.

A.3.2 Immersion Time

Measurements of hours wet per day were made once for each plot at Neponset River. All but one of the tidal meters deployed in Barnstable Harbor were either lost or leaked and malfuctioned. Data collected previously (1–5/97) at one of the plots at Barnstable can be used, so we have data for two plots at Barnstable Harbor, specifically, 20.7 (plot 1) and 11.2 (plot 4) hours wet/day (mean=15.95, variance=45.12). Water coverages at Neponset were 21.7, 18.9, 22.9, 17.2, and 18.3 (plots 1–5) hours per day (mean=19.8, variance=5.76). A t–test comparing means at the two sites was not significant (p=0.27).

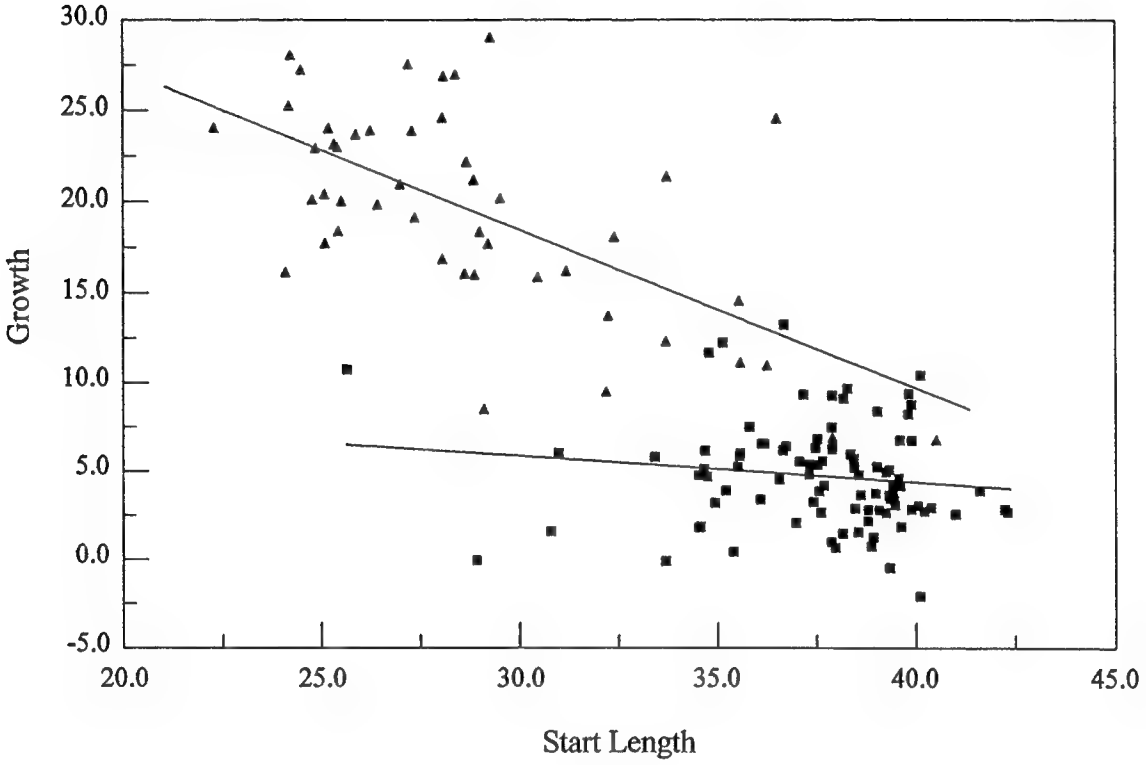

Figure A.2: Growth by start length. Growth (mm/3 mo) for each clam is plotted against its length at the start of the study. Triangles are clams from Barnstable Harbor and squares are clams from Neponset River.

Table A.3: ANOVA table for mud fraction of sediments. Source of variation (Source) is explained by the sum of squares (SS), degrees of freedom (*df*), mean square (MS), F statistic (F), and significance (p).

Source	SS	*df*	MS	F	p
Among sites	0.001	1	0.001	0.111	>0.05
Among plots within sites	0.072	8	0.009	45	<0.001
Within plots	0.002	10	0.0002		
Total	0.075	19			

A.3.3 Sediment Samples

Sediment Grain Size

Mud fractions of sediments varied between plots, but about the same range (6% to 23%) was represented at each site (Figure A.3). Mud fractions were compared with a nested design ANOVA (Table A.3). No significant variation was found between sites ($p>0.05$), but there was a highly significant ($p<0.001$) added variance component among plots.

Sediment Organic Carbon and Nitrogen

Sediments were about 1% organic carbon (by weight) and about 0.1% nitrogen. The two plots (4 and 6) with high levels of carbon and nitrogen (Figure A.4) are also high in mud content (Figure A.3). Although there was slightly more carbon and nitrogen at Neponset than at Barnstable, the difference between sites was not significant for either factor when tested in a nested design ANOVA (Table A.4). There was a

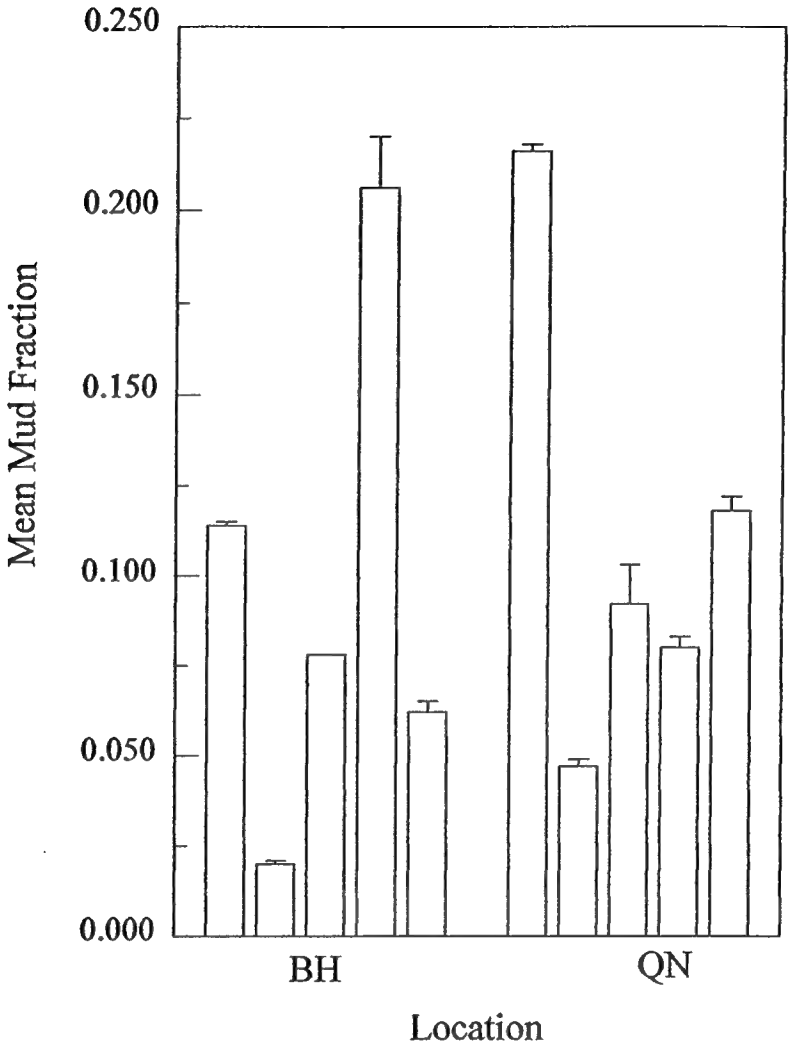

Figure A.3: Sediment Grain Size. Bars show the mean of two replicate samples of mud fraction (g <63μm per gram sediment) for the five plots (1–5, left to right) at Barnstable (BH) and Neponset (QN). Error bars are one standard error.

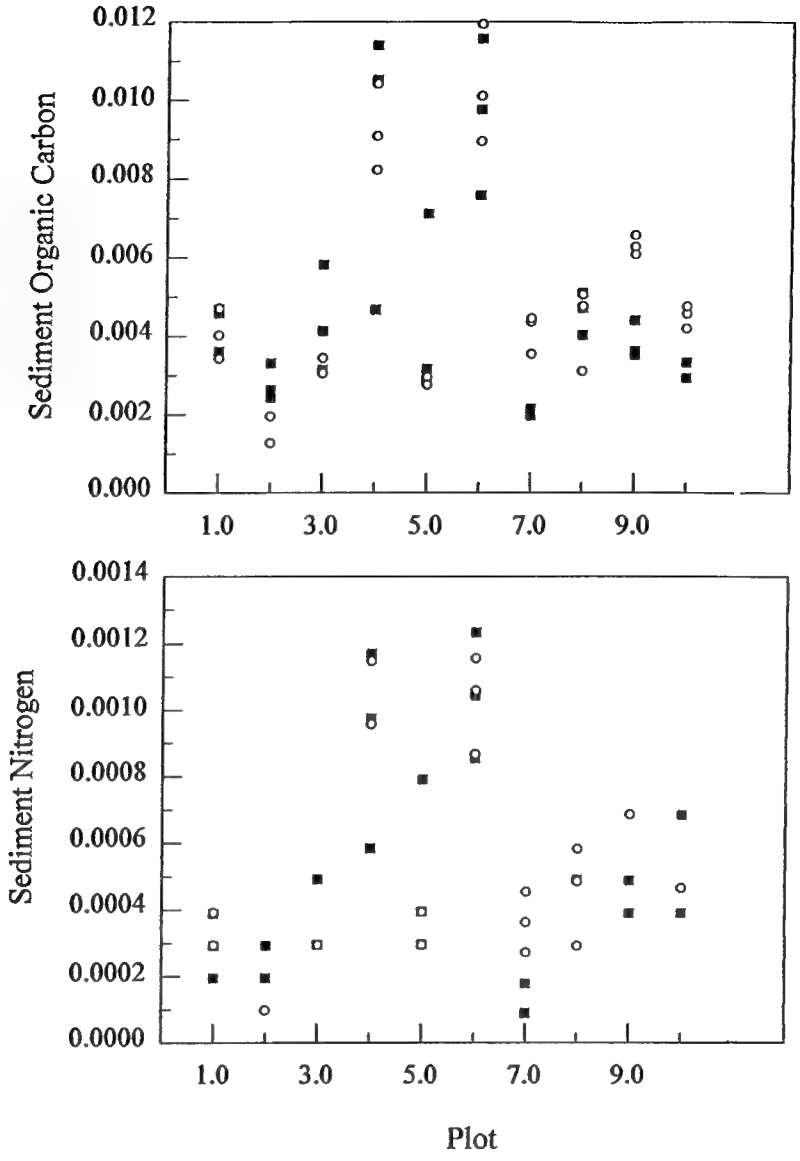

Figure A.4: Sediment organic carbon and nitrogen. Organic carbon (g/g sediment) is shown in the top panel, and nitrogen (g/g sediment) is shown in the lower panel. Points shown are each of three replicate C:H:N anlyses on each sediment sample. Filled squares are one replicate sediment sample from a plot, and open circles in the same column are the other replicate from the same plot. Plots are numbered 1–10, where 1–5 are at Barnstable Harbor and 6–10 are at Neponset River.

significant added variance component for carbon due to both plots ($p<0.01$) and replicates ($p<0.001$), but for nitrogen these factors were not significant ($p>0.05$).

A.4 Discussion

The question this study was designed to answer was whether observed differences in clam growth rates between contaminated and uncontaminated sites were likely due to contaminant levels, or whether they could be explained by some of the many other physical factors that could differ between sites. The results of this study reinforced our previous results (Ripley and McDowell, in prep.) in that clam growth rates at Barnstable Harbor, the uncontaminated site, were higher than at Neponset River, the contaminated site. The significance of this difference could not be evaluated due to differences in size of clams used at each site, however, in the size range that was represented at both sites (30–35 mm), clams at Barnstable Harbor grew about 10 mm more than clams at Neponset River did in the three month period. This difference in growth could mean that clams at Barnstable reached reproductive size (ca. 40 mm: Belding, 1930) a year before Neponset River clams and is probably an important difference, regardless of statistical significance.

Evaluating whether the observed difference in growth rates between sites could be due to any factor known to influence growth rates in bivalves besides contaminant levels was the real object of this study. These factors are sediment composition (Appledoorn, 1981), submergence time (Lin, 1989), and food availability (Judge *et al.*, 1992). We showed that mud fractions of sediments varied among plots at both sites, but did not differ between sites. Sediment composition thus does not explain the observed pattern of clam growth rates. Submergence times did not differ between sites, either. Although data were incomplete at Barnstable Harbor, missing data points would all have to be close to the lower value to change the significance of the test. This would mean that submergence times would be significanlty lower at

Table A.4: ANOVA table for organic carbon and nitrogen in sediments. Source of variation (Source) is explained by the sum of squares (SS), degrees of freedom (df), mean square (MS), F statistic (F), and significance (p).

Source	SS	df	MS	F	p
Organic Carbon					
Among sites	1	1.44×10^{-5}	1.44×10^{-5}	0.36	>0.05
Among plots w/in sites	8	3.08×10^{-4}	3.85×10^{-5}	5.0	<0.01
Among reps w/in plots	10	7.7×10^{-5}	7.7×10^{-6}	7.0	<0.001
W/in reps	40	4.4×10^{-5}	1.1×10^{-6}		
Total	59	4.43×10^{-4}			
Nitrogen					
Among sites	1	1.06×10^{-6}	1.06×10^{-6}	2.97	>0.05
Among plots w/in sites	8	2.86×10^{-6}	3.57×10^{-7}	2.13	>0.05
Among reps w/in plots	10	1.68×10^{-6}	1.68×10^{-7}	67.2	>0.05
W/in reps	40	1.0×10^{-7}	2.5×10^{-9}		
Total	59	5.69×10^{-6}			

Barnstable Harbor, which does not explain the pattern of growth rates, because lower submergence times should lead to lower growth rates (Lin, 1989).

Sediment nitrogen levels were measured as an approximation to food content of the overlying water. No differences were found between sites, or between plots, demonstrating that differences in growth would not be correlated to differences in sediment nitrogen. Sediment nitrogen may not be a good enough aproximation to food supply to the clams. Measuring actual chlorophyll *a* content in water overlying mud flats has been shown to explain growth patterns (Grizzle and Morin, 1989), but this method was beyond the scope of our interest in this question. Similarly, total organic carbon content of sediments is only an approximate measure of lipophilic organic contaminant concentrations. Carbon was not shown to differ between sites, but high variation between sub-samples could have made site differences undetectable. However, according to our measurements, organic carbon could not explain differences in growth rates, either.

A factor we did not evaluate that could play a role in growth rates are genetic differences between sites (Rawson and Hilbish, 1991). It is possible that clams at Barnstable are a faster–growing strain, and it would be interesting to investigate this question further. It is also possible that some other environmental factor that we did not measure is responsible for determining clam growth rates, although all factors previously demonstrated to be important to bivalve growth were measured in some way. The methods we used to measure clam food supply and sediment organic contaminants were only approximations, however, and more conclusive results might be found using more accurate techniques.

A.5 Summary

None of the measured environmental factors (sediment organic carbon, sediment nitrogen, sediment mud fraction, immersion time) showed the same pattern of consis-

tently higher values at Barnstable Harbor plots as did clam growth rates.

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16. Abstract (Limit: 200 words)

In this dissertation, I investigated how the life history characteristics of the clam *Mya arenaria* determine population responses to chronic contaminant exposure. For marine bivalves, the two dominant modes of reproduction are to broadcast gametes into the water or to brood the developing embryos inside the shell. Matrix models were used to determine (from literature data on a range of species) that life span and size are the principal indicators of whether brooding or planktonic development for larvae is the reproductive strategy of a bivalve species. One consequence of the broadcast spawning strategy of *M. arenaria* is that juvenile recruitment to a population is uncertain. However, I showed in a stochastic matrix population model that longer life span allows populations to persist through years of low recruitment and to profit from the large, rare recruitment pulses possible with copious production of planktonic larvae. Finally, data collected on clam vital rates at contaminated and uncontaminated sites showed that recruitment history and other ecological factors, such as predation pressure, determine dynamics of populations under chronic contaminant exposure to a greater degree than do physiological impairments of adults. Contaminant effects are strongest on factors that are not particularly important to population processes in clams.

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